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THE GENERA OF ARABIDEAE (CRUCIFERAE; BRASSICACEAE) IN THE SOUTHEASTERN UNITED STATES[1,2]

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Tribe **Arabideae** A. P. de Candolle, Syst. Nat. **2:** 146, 161. 1821.

Annual, biennial, or perennial herbs [rarely subshrubs], glabrous or with simple, furcate, stellate, or dendritic [very rarely malpighiaceous or glandular] trichomes. Inflorescences ebracteate or bracteate, corymbose racemes or rarely panicles, usually elongated in fruit; flowers sometimes solitary on very long

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The illustrations in FIGURE 3 (a, b, d–f) were drawn by the late Dorothy H. Marsh (DHM); those in FIGURES 1 (a–e, g–l) and 3 (h, i) by Karen Stoutsenberger (KS) under earlier grants. Carroll Wood prepared the material and supervised the illustrations. The remaining illustrations (FIGURES 1f, m, n; 2; 3c, g) were drawn by me (IAS). The fruits and seeds are from herbarium specimens in the Arnold Arboretum and the Gray Herbarium.

[2] For an account of the family and its tribes, see Al-Shehbaz, The tribes of the Cruciferae (Brassicaceae) in the Southeastern United States. Jour. Arnold Arb. **65:** 343–373. 1984.

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peduncles arising from basal rosettes. Sepals erect to spreading, not saccate or strongly saccate at base. Stamens 6, often tetradynamous; filaments free [or very rarely connate], slender [or very rarely broadly winged and/or appendaged]. Fruits dehiscent, linear or sometimes lanceolate, oblong, ovate, or globose, flattened parallel to the septum or sometimes terete; valves glabrous or pubescent, with a prominent or obscure midnerve; septum complete or with a central perforation; styles long to obsolete; stigmas entire to prominently 2-lobed. Seeds several to numerous, uniseriately or biseriately arranged in each locule, mucilaginous or not when wet, winged to marginate or wingless; cotyledons accumbent or very rarely incumbent. (Including Cardamineae Dumort., Selenieae Torrey & A. Gray.) TYPE GENUS: *Arabis* L.

The Arabideae contain some 36 genera and about 615 species, 460 (75 percent) of which belong to three genera: the circumboreal *Arabis* (180 species), the cosmopolitan *Cardamine* L. (200), and *Rorippa* Scop. (80), which form the core of the tribe. Twelve genera are monotypic, and 12 others have two to four species each. About 15 genera of the Arabideae are endemic to central Asia and adjacent Bhutan, China, and Nepal; nine to North America and Mexico; and one each to the Caucasus, southwestern Asia, southern Europe, South America, South Africa, and New Zealand.

Nearly half of the genera included in the Arabideae by earlier authors (e.g., De Candolle (1821, 1824); Bentham & Hooker; Von Hayek) are now assigned to other tribes. Schulz defined the tribe on the basis of its open calyces with ascending or spreading sepals, its long, many-seeded fruits that are usually compressed parallel to the septum, and its embryos with accumbent cotyledons. He relied heavily on the orientation of sepals for the separation of the Arabideae from the Matthioleae O. E. Schulz and on the cotyledonary position for the separation of both of these from the Hesperideae Prantl. Because of the rigid adherence by some authors to these sets of characters, some reasonably well-defined genera were subdivided into several segregates, while other, closely related ones were placed in separate tribes. A case in point involves the genera *Christolea* Camb., *Ermania* Cham., and *Parrya* R. Br., which have been divided into 16 segregates placed in the three tribes above (Botschantzev, 1955, 1972). It is beyond the scope of this flora to evaluate these segregates or to assign them to tribes.

The limits of the Arabideae adopted here follow those of Schulz, except for the reduction of six genera to synonymy and the assignment of nine others, including *Selenia* Nutt. and *Armoracia* Gaertner, Meyer, & Scherb., to this tribe. Although Schulz placed *Selenia* in the Lunarieae O. E. Schulz and *Armoracia* in the Drabeae O. E. Schulz, it is evident that they are closely related respectively to *Leavenworthia* Torrey and *Rorippa,* genera that have been assigned to the Arabideae by many authors, including Schulz.

The Arabideae are represented in the southeastern United States by nine genera and 47 species, all but nine of which are indigenous. Six species and three varieties are endemic, and the ranges of four species and of most taxa of *Leavenworthia* are centered in the Southeast.

Chromosome numbers are known for some 260 species (about 42 percent

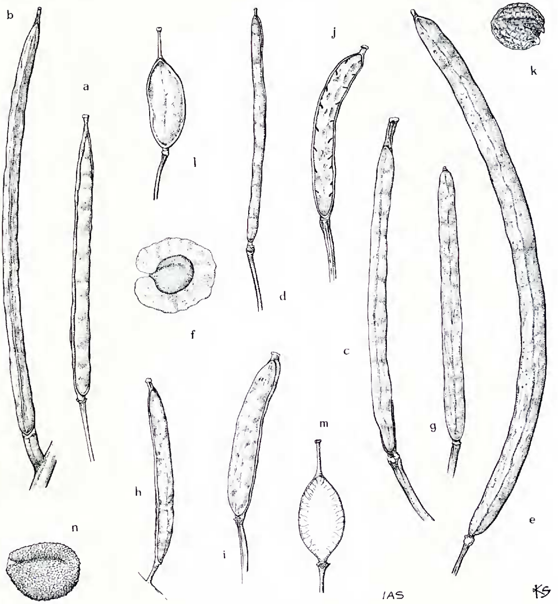

FIGURE 1. Fruits and seeds of Arabideae. a, *Cardamine rhomboidea,* fruit, × 3. b, *Barbarea verna,* fruit, × 2. c, *Iodanthus pinnatifidus,* fruit, × 3. d, *Arabis lyrata,* fruit, × 3. e, f, *A. canadensis:* e, fruit, × 2; f, seed, × 7. g, *Sibara virginica,* fruit, × 3. h, *Rorippa teres,* fruit, × 3. i–k, *R. Nasturtium-aquaticum:* i, fruit, × 3; j, replum and septum, × 3—note funicles of biseriately arranged seeds; k, seed, × 12. l–n, *Armoracia lacustris:* l, fruit, × 3; m, septum and replum, × 3—note central perforation and numerous funicles; n, seed, × 25.

of the tribe) and 18 genera. Nearly 66 percent of the species surveyed have chromosome numbers based on eight, and 20 percent are based on seven. About 52 percent of the species are diploid, while nearly 40 percent are exclusively polyploid (author's compilation). On the basis of the presence of $n = 12$ in a few species of *Rorippa* (as *Nasturtium* R. Br.), Mukherjee concluded that the base chromosome number for the Arabideae is six. His findings, however, are not supported by the data above.

The tribe has been poorly studied for chemical constituents. The seeds of only 40 species, about 30 of which belong to *Arabis,* have been analyzed for fatty acids. The scant data show certain patterns of potential chemotaxonomic value at the generic level. The glucosinolate profiles of about 30 species have been determined. The presence of high methylthioalkyl and methylsulfinylalkyl glucosinolates in *Arabis, Rorippa, Sibara* Greene, and *Drabopsis* C. Koch (monotypic, Southwest Asia) supports the disposition of these genera in the same tribe (MacLeod & MacLeod; Al-Shehbaz & Al-Shammary). However, more species of the first two and of other genera, particularly *Cardamine,* need to be surveyed before any fruitful conclusions can be reached. Several species of *Arabis, Cardamine,* and *Rorippa* have been analyzed for flavonoids, but the data are too fragmentary for meaningful generalizations.

Various members of the Arabideae have dispersal mechanisms similar to those of other tribes. The only exception is *Cardamine,* which has explosive fruits with elastic, spirally coiling valves. Schulz stated that *Loxostemon* J. D. Hooker & Thomson (four species; Bhutan, Sikkim, southern China) resembles *Cardamine* in fruit dehiscence but differs in its winged, spreading or reflexed staminal filaments (slender, wingless, and erect in the latter genus).

Although species of the Arabideae grow in diverse habitats, the majority occupy mesic environments. Several species of *Rorippa* and *Cardamine* are submersed or floating aquatics. The tribe has no xerophytic representatives. Many genera, such as *Anelsonia* Macbride & Payson (monotypic; Idaho, Nevada, California) and *Pegaeophyton* Hayek & Hand.-Mazz. (four species; Himalayas), which are scapigerous, cespitose perennials with thick rootstocks, are exclusively alpine.

Some of the economically important crops of the Arabideae are horseradish (*Armoracia rusticana* Gaertner, Meyer, & Scherb.) and watercress (*Rorippa Nasturtium-aquaticum* (L.) Hayek). Several species of *Arabis* (rockcress) and *Cardamine* (bittercress) are ornamentals, and many of the latter genus and of *Barbarea* R. Br. are widespread weeds.

REFERENCES:[4]

Under family references in AL-SHEHBAZ (Jour. Arnold Arb. **65:** 343–373. 1984), see BAILLON; BENTHAM & HOOKER; BUSCH; DE CANDOLLE (1821, 1824); VON HAYEK; HEDGE & RECHINGER; HEWSON; JAFRI; JANCHEN; JARETZKY (1932); MANTON; MARAIS; ROLLINS (1981); SCHULZ; and SMALL.

AL-SHEHBAZ, I. A. Protogyny in the Cruciferae. Syst. Bot. **2:** 327–333. 1977. [*Arabis, Armoracia, Barbarea, Cardamine, Rorippa.*]

———. The tribes of the Cruciferae (Brassicaceae) in the southeastern United States. Jour. Arnold Arb. **65:** 343–373. 1984.

——— & K. I. AL-SHAMMARY. Distribution and chemotaxonomic significance of glucosinolates in certain Middle-Eastern Cruciferae. Biochem. Syst. Ecol. **15:** 559–569. 1987. [*Arabis, Barbarea, Drabopsis.*]

APPELQVIST, L.-A. Lipids in Cruciferae: VIII. The fatty acid composition of seeds of some wild or partially domesticated species. Jour. Am. Oil Chem. Soc. **48:** 740–744. 1971. [*Arabis, Barbarea, Cardamine.*]

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[4] In the annotated references below the genera *Arabis, Cardamine,* and *Rorippa,* include *Turritis* L., *Dentaria* L., and *Nasturtium,* respectively.

BEAL, E. O. A manual of marsh and aquatic vascular plants of North Carolina with habitat data. North Carolina Agr. Exp. Sta. Tech. Bull. **247.** iv + 298 pp. 1977. [*Armoracia, Cardamine, Rorippa,* 188–191.]

BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA, & O. ZAKHARYEVA. Chromosome numbers of flowering plants. A. A. FEDOROV, ed. (Russian and English prefaces.) 926 pp. Leningrad. 1969. [*Arabis, Armoracia, Barbarea, Cardamine, Rorippa,* 163–177.]

BOTSCHANTZEV, V. De cruciferis notae criticae. (In Russian.) Notul. Syst. **17:** 160–178. 1955. [*Christolea, Ermania, Eurycarpus, Parrya, Parryopsis, Phaeonychium, Solms-Laubachia, Vvedenskyella.*]

———. On *Parrya* R. Br., *Neuroloma* Andrz. and some other genera (Cruciferae). (In Russian.) Bot. Zhur. **57:** 664–673. 1972. [*Ermania, Leiospora, Neuroloma, Oreoblastus, Pachyneurum, Parrya.*]

CHESTER, E. W. Range extensions and first reports for some Tennessee vascular plants. Castanea **40:** 56–63. 1975. [*Arabis, Armoracia, Cardamine, Rorippa,* 59.]

CLEWELL, A. F. Guide to the vascular plants of the Florida panhandle. viii + 605 pp. Tallahassee, Florida. 1985. [*Arabis, Armoracia, Cardamine, Rorippa, Sibara,* 337–343.]

COLE, R. A. Isothiocyanates, nitriles and thiocyanates as products of autolysis of glucosinolates in Cruciferae. Phytochemistry **15:** 759–762. 1976. [*Arabis, Barbarea, Cardamine, Rorippa.*]

CORBETT, G. A. New records for the West Virginia Cruciferae. Castanea **38:** 214–229. 1973.

CORRELL, D. S., & H. B. CORRELL. Aquatic and wetland plants of southwestern United States. xv + 1777 pp. 1972. (Reissued in two volumes. Stanford. 1975.) [*Arabis, Armoracia, Barbarea, Cardamine, Iodanthus, Leavenworthia, Rorippa, Selenia, Sibara,* 962–984.]

DAXENBICHLER, M. E., C. H. VANETTEN, F. S. BROWN, & Q. JONES. Oxazolidinethiones and volatile isothiocyanates in enzyme-treated seed meals from 65 species of Cruciferae. Agr. Food Chem. **12:** 127–130. 1964. [*Arabis, Barbarea, Rorippa, Selenia.*]

DUNCAN, W. H., & J. T. KARTESZ. Vascular flora of Georgia. ix + 143 pp. Athens, Georgia. 1981. [*Arabis, Armoracia, Barbarea, Cardamine, Leavenworthia, Rorippa, Sibara,* 62–64.]

ELLIS, W. H., E. WOFFORD, & E. W. CHESTER. A preliminary checklist of the flowering plants of the Land between the Lakes. Castanea **36:** 229–246. 1971. [*Arabis, Armoracia, Cardamine, Iodanthus, Rorippa, Sibara,* 237; Stewart County, Tennessee.]

FASSETT, N. C. A manual of aquatic plants. 382 pp. New York and London. 1940. [*Armoracia* (as *Neobeckia*), *Cardamine, Rorippa,* 228–237.]

FREEMAN, J. D., A. S. CAUSEY, J. W. SHORT, & R. R. HAYNES. Endangered, threatened, and special concern plants of Alabama. 25 pp. Auburn, Alabama. 1979. [*Arabis, Armoracia, Leavenworthia,* 6, 12, 20, 25.]

GATTINGER, A. The flora of Tennessee and a philosophy of botany. 294 pp. Nashville, Tennessee. 1901. [*Arabis* (including *Sibara*), *Cardamine, Iodanthus, Leavenworthia, Rorippa* (including *Armoracia*), 86–89.]

GODFREY, R. K., & J. W. WOOTEN. Aquatic and wetland plants of southeastern United States. Dicotyledons. x + 933 pp. Athens, Georgia. 1981. [*Armoracia, Cardamine, Iodanthus, Rorippa,* 170–183.]

GOLDBLATT, P., ed. Index to plant chromosome numbers 1975–1978. Monogr. Syst. Bot. **5.** vii + 553 pp. 1981. [*Arabis, Barbarea, Cardamine, Rorippa,* 152–161.]

———, ed. Index to plant chromosome numbers 1979–1981. *Ibid.* **8.** viii + 427 pp. 1984. [*Arabis, Armoracia, Barbarea, Cardamine, Rorippa,* 116–124.]

———, ed. Index to plant chromosome numbers 1982–1983. *Ibid.* **13.** vii + 224 pp. 1985. [*Arabis, Barbarea, Cardamine, Rorippa,* 63–67.]

GOLUBKOVA, V. P. System of the genus *Dontostemon* Andrz. ex C. A. Mey. (Cruciferae). (In Russian.) Bot. Zhur. **59:** 1638, 1639. 1974. [A related paper in Acta Inst. Bot. Acad. Sci. USSR **9:** 71–106. 1950.]

HEBEL, M. The mustards and related plant families in eastern Tennessee. Part II. Taxonomy. Jour. Tenn. Acad. Sci. **8:** 382–417. 1933. [*Arabis* (including *Sibara*), *Barbarea, Cardamine, Iodanthus, Leavenworthia, Rorippa* (as *Radicula,* including *Armoracia*), 394–403.]

JONES, S. B., JR. The flora and phytogeography of the Pine Mountain region of Georgia. Castanea **39:** 113–149. 1974. [*Arabis, Cardamine, Rorippa,* 130.]

———. Mississippi flora. III. Distribution and identification of the Brassicaceae. *Ibid.* **40:** 238–252. 1975. [*Arabis, Armoracia, Barbarea, Cardamine, Rorippa, Sibara*; keys, maps.]

KJAER, A. Naturally derived isothiocyanates (mustard oils) and their parent glucosides. Fortschr. Chem. Organ. Naturstoffe **18:** 122–176. 1960. [*Arabis, Armoracia, Barbarea, Cardamine, Rorippa.*]

LITCHFIELD, C. The α, β-distribution of oleic, linoleic and linolenic acids in Cruciferae seed triglycerides. Jour. Am. Oil Chem. Soc. **48:** 467–472. 1971. [*Arabis, Barbarea, Rorippa.*]

MACBRIDE, J. F., & E. B. PAYSON. *Anelsonia,* a new genus of the Cruciferae. Bot. Gaz. **64:** 79–81. 1917. [*Parrya, Phoenicaulis,* relationships and distinguishing characters.]

MACLEOD, A. J., & G. MACLEOD. Synthesis and natural occurrence of 8-methylthiooctanonitrile and 9-methylthiononanonitrile. Phytochemistry **16:** 907–909. 1977. [*Arabis, Rorippa, Sibara.*]

MACROBERTS, D. T. The vascular plants of Louisiana. An annotated checklist and bibliography of the vascular plants reported to grow without cultivation in Louisiana. Bull. Mus. Life Sci. Louisiana State Univ. Shreveport **6:** 1–165. 1984. [*Arabis, Armoracia, Barbarea, Cardamine, Rorippa, Sibara.*]

MATTHEWS, J. F., R. L. KOLOGISKI, T. L. MELLICHAMP, *et al.* Additional records to the vascular flora of the Carolinas. Castanea **39:** 349–360. 1974. [*Arabis, Barbarea, Cardamine,* 352.]

MCKINNEY, L. E. The vascular flora of Short Mountain (Cannon County) Tennessee. Jour. Tenn. Acad. Sci. **61:** 20–24. 1986. [*Arabis, Barbarea, Cardamine, Iodanthus, Rorippa.*]

MIKOLAJCZAK, K. L., T. K. MIWA, F. R. EARLE, I. A. WOLFF, & Q. JONES. Search for new industrial oils. V. Oils of Cruciferae. Jour. Am. Oil Chem. Soc. **38:** 678–681. 1961. [*Arabis* (including *Sibara*), *Rorippa, Selenia.*]

MILLER, R. W., F. R. EARLE, I. A. WOLFF, & Q. JONES. Search for new industrial oils. XIII. Oils from 102 species of Cruciferae. Jour. Am. Oil Chem. Soc. **42:** 817–821. 1965. [*Arabis, Barbarea, Cardamine, Leavenworthia.*]

MOHR, C. Plant life of Alabama. xii + 921 pp. Montgomery, Alabama. 1901. (Reprinted from Contr. U. S. Natl. Herb. Vol. 6. 1901.) [*Arabis, Cardamine, Iodanthus, Leavenworthia, Rorippa, Sibara* (as *Arabis*), 524–528.]

MOORE, R. J., ed. Index to plant chromosome numbers 1967–1971. Regnum Veg. **90:** 1–539. 1973. [*Arabis, Barbarea, Cardamine, Rorippa, Selenia, Sibara,* 202–211.]

MUKHERJEE, P. Chromosome study as an aid in tracing the evolution of Cruciferae. Cytologia **40:** 727–734. 1975. [Counts for 20 species, karyotype analysis for seven species; the basic number for both Arabideae and Brassiceae is six; roles of aneuploidy and of reduction in chromosome size.]

NIELSEN, J. K., L. DALGAARD, L. M. LARSEN, & H. SØRENSEN. Host plant selection of the horse-radish flea beetle *Phyllotreta armoraciae* (Coleoptera: Chrysomelidae): feeding responses to glucosinolates from several crucifers. Entomol. Exp. Appl. **25:** 227–239. 1979. [*Armoracia, Cardamine, Rorippa.*]

PATMAN, J. A checklist of Florida Cruciferae. Quart. Jour. Florida Acad. Sci. **25:** 192–200. 1962. [*Armoracia, Cardamine, Rorippa, Sibara.*]

PULLEN, T. M., S. B. JONES, JR., & J. R. WATSON, JR. Additions to the flora of Mississippi. Castanea **33:** 326–334. 1968. [*Armoracia, Cardamine, Rorippa,* 329.]

ROLLINS, R. C., E. A. SHAW, & R. J. DAVIS. Cruciferae. Pp. 671–706 *in* D. S. CORRELL

& M. C. Johnston, Manual of the vascular plants of Texas. Renner, Texas. 1970. [*Arabis, Cardamine, Iodanthus, Leavenworthia, Rorippa, Selenia, Sibara.*]

Sharp, A. J., R. E. Shanks, H. L. Sherman, & D. H. Norris. A preliminary checklist of dicots in Tennessee. 114 pp. Mimeographed. Univ. Tennessee, Knoxville. 1960. [*Arabis, Barbarea, Cardamine, Iodanthus, Leavenworthia, Rorippa, Sibara,* 20–22.]

Small, J. K. Flora of the southeastern United States. xii + 1370 pp. New York. 1903. [*Arabis* (including *Sibara*), *Barbarea, Cardamine, Iodanthus, Leavenworthia, Rorippa* (including *Armoracia*), *Selenia,* 472–486.]

Stace, C. A., ed. Hybridization and the flora of the British Isles. xiii + 626 pp. London, New York, and San Francisco. 1975. [*Arabis, Barbarea, Cardamine, Rorippa,* 147–153.]

Thompson, R. L. The vascular flora of Lost Valley, Newton County, Arkansas. Castanea **42:** 61–94. 1977. [*Arabis, Barbarea, Cardamine, Rorippa,* 79, 80.]

Van Horn, G. S. A checklist of the vascular plants of Chickamauga and Chattanooga National Military Park. Jour. Tenn. Acad. Sci. **56:** 92–99. 1981. [*Arabis, Barbarea, Cardamine,* 96.]

Key to the Genera of Arabideae in the Southeastern United States[5]

A. Early flowers solitary, borne on scapes 3–10 cm long originating from the center of a basal rosette; radicle straight or slightly curved, much shorter than the cotyledons. .... 30. *Leavenworthia.*

A. All flowers borne in corymbose racemes, racemes, or panicles; radicle strongly curved, about as long as the incumbent or accumbent cotyledons.

  B. Fruits at least 4 times longer (usually much more) than broad, linear or narrowly oblong.

    C. Plants with stellate or variously furcate trichomes, sometimes also with unbranched ones. .... 32. *Arabis.*

    C. Plants glabrous or with unbranched trichomes only.

      D. Fruits flattened parallel to septum; petals never yellow.

        E. Valves of fruits dehiscing suddenly and elastically, coiling spirally or circinately; replums narrowly winged; seeds neither winged nor marginate; plants perennials with tubers or rhizomes, sometimes annuals. ... . 27. *Cardamine.*

        E. Valves neither dehiscing elastically nor coiling; replums wingless; seeds winged, marginate, or wingless; plants (ours) biennials or annuals.

          F. Cauline leaves entire or toothed; median nectar glands usually present. .... 32. *Arabis.*

          F. Cauline leaves pinnatisect; median nectar glands absent. .... 33. *Sibara.*

      D. Fruits terete or quadrangular, rarely slightly flattened; petals yellow, white, or lavender.

        G. Valves of fruits with a prominent midvein; seeds uniseriately arranged in each locule.

          H. Flowers yellow; inflorescences corymbose; cauline leaves auriculate to amplexicaul, not cuneate. .... 28. *Barbarea.*

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[5] The genera are numbered as in the treatment of the tribes of the Cruciferae in the southeastern United States (Jour. Arnold Arb. **65:** 343–373. 1984). Genera 1 and 2 (Thelypodieae) appeared in *ibid.* **66:** 95–111. 1985; genera 3–13 (Brassiceae) in *ibid.* 279–351; genera 14–19 (Lepidieae) in *ibid.* **67:** 265–311. 1986; and genera 20–26 (Alysseae) in *ibid.* **68:** 185–240. 1987.

Nasturtium, genus 34 in my key to the genera of the Cruciferae (Jour. Arnold Arb. **65:** 367. 1984), is united in this treatment with *Rorippa* (genus 35) for reasons given below.

H. Flowers white or lavender; inflorescences elongated racemes; cauline leaves cuneate. . . . . 29. *Iodanthus.*

G. Valves nerveless or obscurely nerved; seeds biseriately arranged or, if uniseriate, the plants aquatic. . . . . 35. *Rorippa.*

B. Fruits less than 3 times longer than broad, globose, elliptic, or broadly oblong.

I. Inflorescences bracteate throughout; seeds broadly winged; fruits usually compressed parallel to septum. . . . . 31. *Selenia.*

I. Inflorescences ebracteate; seeds wingless; fruits somewhat inflated.

J. Flowers yellow; septum complete; plants annual or biennial, rarely perennial. . . . . 35. *Rorippa.*

J. Flowers white; septum rudimentary or with a central perforation; plants perennial. . . . . 36. *Armoracia.*

27. **Cardamine** Linnaeus, Sp. Pl. 2: 654. 1753; Gen. Pl. ed. 5. 295. 1754.

Herbaceous annuals, biennials, or rhizomatous or tuberous perennials, glabrous or with unbranched trichomes only. Rhizomes (when present) fleshy or not, scaly or not, continuous or obscurely to conspicuously constricted or moniliform, sometimes readily separated into fusiform to ellipsoid segments, occasionally with clusters of small, stalked or sessile tubers. Stems erect to ascending to decumbent, sometimes rooting from the lower nodes. Basal or rhizomal leaves rarely forming distinct rosettes, petiolate, entire or ternately, palmately, or pinnately lobed or dissected, occasionally resembling compound leaves. Cauline leaves alternate or very rarely opposite or whorled, petiolate or sessile, rarely auriculate at base. Inflorescences bracteate or ebracteate corymbose racemes or panicles, usually greatly elongated in fruit. Sepals erect to spreading, oblong to ovate, often membranaceous at margin, the lateral pair saccate or not saccate at base. Petals white, lavender, rose, purple, or violet, never yellow, erect or spreading, obovate to spatulate, entire to emarginate, clawed or gradually narrowed to a clawlike base, sometimes absent. Lateral nectar glands usually well developed, horseshoe shaped or ringlike, surrounding or subtending the base of single stamens; median glands flat or toothlike, usually 1, rarely 2 or absent. Stamens 6, slightly to strongly tetradynamous, rarely 4; filaments free, erect or spreading, unappendaged; anthers ovate or oblong to linear, usually sagittate at base. Fruits dehiscent, linear to narrowly lanceolate, straight, smooth to torulose, flattened parallel to the septum or rarely subterete, gradually to abruptly narrowed to style; valves glabrous [or very rarely pubescent], dehiscing elastically from the base upward, often circinately or spirally coiled, not veined or sometimes the basal portion with an obscure midnerve; replum broad, persistent, always narrowly winged; septum hyaline, complete; styles long and often beaklike or short to obsolete; stigmas capitate, slightly 2-lobed. Seeds numerous to rarely few, compressed, oblong to ovate, smooth or rugose to reticulate or colliculate, uniseriately arranged in each locule, usually neither winged nor marginate, mucilaginous or nonmucilaginous when wet; cotyledons accumbent or very rarely incumbent, equal or unequal, sessile to petiolate. Base chromosome numbers 6, 7, 8, 10, 12. (Including *Dentaria* L.;[6]

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[6] *Dentaria* and *Cardamine* were simultaneously described by Linnaeus (Sp. Pl. 2: 653, 654, respectively. 1753). Crantz, who was the first to unite the two genera, adopted *Cardamine* for the combined genus, and consequently this name has priority (see ICBN Article 57.2. 1983).

Dracamine Nieuwl.; *Ghinia* Bubani, non Schreber; *Heterocarpus* Phil., non Wight; *Porphyrocodon* J. D. Hooker; *Pteroneurum* DC.) LECTOTYPE SPECIES: *C. pratensis* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 183. 1913. (Name derived from Greek *kardamon,* used by Dioscorides for some cresses.)—BITTERCRESS, CRINKLEROOT, PEPPERROOT, TOOTHWORT.

A natural and well-defined genus of at least 200 species, but Biswas's estimate of 330 species is evidently exaggerated. *Cardamine* is a cosmopolitan genus represented by indigenous species on all continents except Antarctica. It is poorly represented in the Southern Hemisphere, with only about 30 species in South America, ten in New Zealand and Australia, and three each in New Guinea and Africa. The South American species were reduced to only five by Sjöstedt, who adopted a very broad and rather loose species concept, but the actual number may well exceed 30. The center of greatest diversity is the Far East and the Himalayas, where about 70 representatives grow. The genus is also well developed in North and Central America (40 species) and Europe (25). About ten species are widely distributed in Eurasia and/or North America; only four are cosmopolitan weeds. Most taxa grow in wet habitats, alpine areas, and forests; some are aquatic, and none are xerophytes. The great majority are rhizomatous or tuberous perennials, and only about 15 percent of the species are annuals (author's compilation). *Cardamine* is represented in the southeastern United States by 13 indigenous and two naturalized species.

The sectional classification of *Cardamine* is controversial. Schulz (1903, 1936) recognized as many as 13 sections, six of which are monotypic. He overemphasized a few characters of the rhizome (such as shape, fleshiness, pubescence, and scaliness) in defining several of his sections. Careful evaluation of these and the other characters used reveals that Schulz's sections have artificial boundaries and often do not represent natural subdivisions of the genus.

Cardamine and *Dentaria* have been recognized as closely related genera by most North American botanists, who have treated them only for local floras and without critical evaluation of their limits on a worldwide basis. *Dentaria* has been said to differ from *Cardamine* in having larger flowers, fleshier and larger rhizomes, fewer, often palmately divided cauline leaves, and usually petiolate cotyledons (Detling, 1936). On the basis of careful examination of the whole complex, however, it is evident that these alleged differences are neither consistent nor reliable. The taxonomy of *Cardamine* cannot be improved by treating *Dentaria* as a genus on the basis of characters that hold only within a small portion of its geographic range. As indicated earlier (Al-Shehbaz, 1988), *Dentaria* should be united with *Cardamine* and does not have to be formally recognized. The combined genus has fruits with a marginate or narrowly winged replum and elastic dehiscence, accompanied by spiral coiling of the valves. These features, which are also found in the very closely related *Loxostemon,* have not been observed elsewhere in the Cruciferae.

Jones (1964) recognized two subgenera in *Cardamine*: subg. *Cardamine* (rhizomes on the surface of the ground, nonscaly or with only a few scales; cotyledons sessile or subsessile) and subg. *Dentaria* (L.) J. D. Hooker (rhizomes subterranean, scaly; cotyledons petiolate). The former includes all species of the genus except the approximately 17 of subg. *Dentaria.* Although some authors recognize infrageneric subdivisions in *Cardamine,* I prefer not to do so pending a thorough systematic study of the entire genus.

Cardamine rhomboidea (Pers.) DC. (*Arabis rhomboidea* Pers., *A. bulbosa* Schreber ex Muhl. (nomen nudum), *C. bulbosa* (Schreber ex Muhl.) BSP., *C. bulbosa* f. *fontinalis* Palmer & Steyerm.), spring cress, $2n = 64, 80, 96, 112(?)$, is quite common in all of the Southeastern States. It grows in wet, low woodlands, floodplain forests, meadows and pastures, marshy areas, low pinelands, and creek bottoms, as well as along stream banks and moist roadsides. It is distributed from Quebec and New Hampshire south to central Florida, west to Texas, and north through Kansas, eastern South Dakota, Minnesota, and southeastern Manitoba. Forma *fontinalis,* known only from Missouri, is merely an aquatic variant that was said to differ from the rest of the species by its nontuberous roots and its broader leaves with a cordate base.

A very close relative of and often confused with the preceding, *Cardamine Douglassii* (Torrey) Britton (*Arabis Douglassii* Torrey, *Dentaria Douglassii* (Torrey) Greene, *A. rhomboidea* Pers. var. *purpurea* Torrey, *C. purpurea* (Torrey) Britton, *Thlaspi tuberosum* Nutt.), purple cress, pink spring cress, $2n = 64, 96, 144$, is distributed from Connecticut south through the Carolinas into Alabama, west to eastern Missouri, north to Wisconsin, and east through Michigan, Ontario, and New York. It is uncommon in the Southeastern States but is known from North Carolina (Durham, Harnett, Northampton, Orange, and Wake counties), South Carolina (Newberry County), Alabama (Clarke, Colbert, Jackson, Lawrence, Madison, Marengo, and Sumter counties), and Tennessee (Cheatham, Davidson, Knox, and Montgomery counties). It grows in calcareous spring-fed places, rich mesic woods and bottomlands, and floodplain woodlands. In general, it is found in areas drier than those occupied by *C. rhomboidea.* Schulz (1903) treated these species as one, with several varieties and forms. Subsequent authors, however, have recognized two species without any infraspecific taxa.

Cardamine Douglassii is distinguished from *C. rhomboidea* by its pink to dark purple (very rarely white) flowers and its trichomes (0.2–)0.3–0.6(–0.8) mm long. *Cardamine rhomboidea* has white flowers and trichomes 0.02–0.1 (–0.2) mm long. It is also taller (15–45 instead of 7–22 cm) and generally flowers two to four weeks after *C. Douglassii.* Both are easily separated from the other eastern North American species of *Cardamine* by their tuberous bases, erect stems, and simple cauline leaves.

Cardamine rotundifolia Michx. (*Dentaria rotundifolia* (Michx.) Greene), mountain watercress, is a mat-forming, stoloniferous, glabrous perennial with erect to decumbent stems that root from the lower nodes; simple, petiolate, broadly ovate to suborbicular leaves that have an entire to repand margin and an obtuse to cordate base; spreading floral parts and distinct fruiting styles to 5 mm long; and divaricately ascending to widely spreading pedicels to 2.5 cm long. It grows along stream sides and in swamps, low woodlands, and spring-fed places in New York south through Pennsylvania to North Carolina (Ashe, Stokes, and Watauga counties) and Georgia (Walker County), west to Tennessee (Carter and Scott counties), and north to Ohio. It can be confused with *C. rhomboidea,* from which it differs in being totally glabrous and in its nontuberous base and spreading floral parts. *Cardamine rotundifolia* is protogynous (pers. obs.) and may be self-incompatible, as is suggested by the lack of fruits among some 40 specimens at the Gray Herbarium.

Cardamine micranthera Rollins, a narrow endemic of North Carolina (Forsyth and Stokes counties), grows in moist woods, seepages, and crevices of outcrops, on moist sandbars, and along stream banks. It is most closely related to *C. rotundifolia,* which it resembles in having spreading floral parts and divaricate fruiting pedicels, but from which it differs in having orbicular anthers ca. 0.5 mm long, narrower petals 1.2–2 mm wide, erect stems without proliferating branches, and smaller fruits 0.8–1.2 cm long. *Cardamine rotundifolia,* on the other hand, has narrowly oblong anthers 1.2–1.6 mm long, lingulate petals 2.5–3.5 mm wide, decumbent stems with proliferating branches, and fruits (1.2–)1.5–2 cm long.

Both *Cardamine flagellifera* O. E. Schulz (*C. Hugeri* Small) and *C. clematitis* Shuttlw. ex A. Gray are endemic to some of the Southeastern States and the adjacent Virginias. A few authors (e.g., Beal, Radford *et al.*) have treated the former (as *C. flagellaris*) as a synonym of the latter, although Schulz (1903) placed them in widely separated sections. In my opinion, the taxa are well-defined, closely related species. They grow in wet woods and spring-fed places, on shady slopes, and along stream banks. *Cardamine clematitis* occurs in Alabama, the Blue Ridge area of Georgia and North Carolina, Tennessee (Blount, Carter, Johnson, Pickett, and Sevier counties), and southwestern Virginia (Grayson, Pulaski, Russell, Smyth, and Washington counties). The range of *C. flagellifera* includes Georgia (Fannin, Rabun, Towns, and White counties), South Carolina (Hog Back Mtn.), North Carolina (Alleghany, Clay, Graham, and Polk counties), Tennessee (Blount, Knox, Polk, and Sevier counties), and West Virginia (Fayette County). Both *C. clematitis* and *C. flagellifera* are rhizomatous perennials with erect stems, reniform or cordate basal leaves, and pinnate cauline leaves with a large, cordate terminal lobe and one or rarely two pairs of smaller, petiolate lateral lobes. *Cardamine flagellifera* is easily distinguished by its stems pubescent on the lower part, its nonauriculate petioles, and its mucronate-crenate leaf lobes. *Cardamine clematitis* has glabrous stems, lanceolate auricles, and entire or obscurely three-angled leaf lobes (FIGURE 2h, i).

Cardamine pensylvanica Muhl. ex Willd. (*C. flexuosa* With. subsp. *pensylvanica* (Muhl. ex Willd.) O. E. Schulz, *C. hirsuta* L. var. *pensylvanica* (Muhl. ex Willd.) Graff, *C. pensylvanica* var. *Brittoniana* Farw.), bittercress, $2n = 32$, 64, is a North American plant widely distributed from Alaska south through British Columbia into northern California, east through Texas to Florida, and north to Newfoundland. It is fairly common throughout the southeastern United States, where it is an aquatic plant of streams, marshes, swamps, ditches, and springs, or a mesophyte of wet grounds along stream banks, in meadows, woodlands, and cultivated fields, and on floodplains. *Cardamine pensylvanica* is quite variable in leaf morphology, particularly in the thickness, width, and number of lateral lobes. In drier habitats it produces many narrow, somewhat fleshy leaf segments, while if submersed or growing in the shade it produces fewer broad, membranaceous ones. Varietas *Brittoniana* is based on aberrant plants with simple upper cauline leaves. The species is distinguished from the other southeastern members of *Cardamine* that have pinnate leaves by its nonciliate petioles, hispid lower stems (glabrous when submersed), lateral lobes with decurrent and oblique bases, somewhat beaked fruits with styles to 2 mm long, and oblong seeds 1–1.5 mm long.

Although several North American authors have recognized *Cardamine parviflora* L. var. *arenicola* (Britton) O. E. Schulz (*C. arenicola* Britton; *C. virginica* Michx., non L.), $2n = 16$, ca. 48, as a distinct species, many others consider it to be a subordinate of the European *C. parviflora.* According to Fernald (1927), var. *arenicola* differs from var. *parviflora* in having basal leaves with dentate, obovate to suborbicular lobes, cauline leaves with fewer (two to six pairs) lobes, slightly more (26–46) ovules, longer petals (2.5–3.5 mm) and fruits (1.5–3 cm), and shorter (4–8 mm) fruiting pedicels. In var. *parviflora* the basal leaves have entire, oblong lobes, the cauline leaves have five to eight pairs of lobes, there are 22–36 ovules, and the petals, fruiting pedicels, and fruits are 2–2.5 mm, 7–10 mm, and 1–2 cm long, respectively.

Varietas *arenicola* usually grows on sandy soil in habitats that are wet for short periods in winter or spring. It occupies low areas in woods, fallow or cultivated fields, pastures, meadows, floodplains, and clearings and on exposed ledges, as well as drier sites along streams, ditches, and roadsides. It is distributed from British Columbia and Oregon east to Newfoundland, south to Florida, and west to Texas and is widespread throughout the Southeastern States. Rollins (1966) reported $n = 22–24$ (indicating hexaploidy) for var. *arenicola* from plants collected in Morgan County, Alabama. Other counts for this variety from North America and for var. *parviflora* from the Soviet Union and Taiwan are diploid ($2n = 16$). More counts are needed to clarify the distribution of the hexaploid plants in the Southeast.

Cardamine hirsuta L., hoary bittercress, $2n = 16$, is a cosmopolitan Eurasian weed that is sporadic in North America and widespread in all of the Southeastern States. It grows in fields, lawns, waste areas, disturbed sites, and clearings, as well as along roadsides, ditches, and stream banks. It is very closely related to *C. flexuosa* With. (*C. hirsuta* var. *flexuosa* (With.) Forbes & Hemsley, *C. debilis* D. Don), $2n = 32$. The latter is another Eurasian annual that is sporadic in eastern North America and has been reported from Florida (Small, 1933; as *C. debilis*) and North Carolina (Radford *et al.*). They differ from the other annual or biennial species of *Cardamine* with pinnate leaves in having ciliate petioles and lowermost leaves often with suborbicular lobes.

According to Ellis & Jones (1969), *Cardamine flexuosa* is an allopolyploid derived from *C. hirsuta* and *C. impatiens* L. ($2n = 16$). The last, a European weed sporadically naturalized from New Hampshire west to Michigan and south to West Virginia (Rollins, 1981), is easily distinguished by its cauline leaves with sagittate-auriculate bases and five to nine pairs of ciliate, lanceolate to ovate, coarsely dentate to incised lateral lobes. *Cardamine hirsuta* differs from *C. flexuosa* in its usually glabrous (instead of densely pubescent) stems, its fewer (two to four vs. four to ten) cauline leaves, its chromosome number (see above), and its usually four (instead of six) stamens. The differences in pubescence and stamen number, however, are not absolute. Jaspars-Schrader has demonstrated that in *C. hirsuta* about 89 percent of the stems are glabrous or nearly so and 11 percent are densely pubescent, while in *C. flexuosa* 87 percent of the stems are densely pubescent and 13 percent are sparsely so. Furthermore, he indicated that 80 percent of the flowers of *C. hirsuta* have four stamens, 18 percent have five, and two percent have six, while 97 percent of those of *C. flexuosa* have six stamens and three percent have five. A combination of six stamens and densely pubescent stems would easily distinguish *C. flexuosa* from *C. hirsuta.*

The occurrence of *Cardamine Longii* Fern. in North Carolina has been established only recently (Sutter *et al.*). It is a rare plant of tidal estuaries, mud flats, and sandy or gravelly fresh tidal shores of rivers along the coasts of Maine and Massachusetts south to Chesapeake Bay, Maryland. It is easily distinguished from all other species of *Cardamine* by its apetalous flowers, reniform to suborbicular or oblong leaves with the base obtuse to cordate, lanceolate to linear fruits 5–12(–18) mm long, and fruiting pedicels 0.5–1.5(–5) mm long (FIGURE 2g).

Several authors (e.g., Small (in family references), Patman, Rickett) have recognized *Cardamine curvisiliqua* Shuttlw. ex Chapman as a member of this genus endemic to Florida. As shown below, however, it is a species of *Rorippa.*

The four remaining species of *Cardamine* in the southeastern United States were previously placed in *Dentaria.* They all flower during the spring and usually grow in nonacidic, usually calcareous soils of rocky banks, wooded bottoms, moist rich woods, shaded slopes, and meadows, as well as along stream banks in woods. *Cardamine diphylla* (Michx.) A. Wood (*Dentaria diphylla* Michx.; *D. bifolia* Stokes; *D. incisa* Small, non Eames), crinkleroot, pepperroot, toothwort, is easily distinguished by its long, nonconstricted, conspicuously scaly rhizomes, its two opposite or sometimes approximately alternate, three-foliolate cauline leaves with subappressed marginal trichomes to 0.1 mm long, and its broadly ovate terminal leaflet 7–10 cm long and 2.5–5 cm wide. It is distributed from Minnesota east through Michigan, southern Ontario, Quebec, and Nova Scotia, south to western North Carolina, South Carolina (Pickens County), northern Georgia, and northern Alabama, and north through Tennessee to Wisconsin. It is very rare and possibly introduced in Arkansas (Yell County) and Missouri (Chariton County). *Cardamine diphylla* has rarely been found to produce fully developed fruits. As was suggested by Harriman (1965), it is difficult to interpret how the species could attain such a wide distribution without the regular production of seeds. He suggested that the failure to produce seeds may be caused by both clonal reproduction and self-incompatibility. The species is weakly protogynous (pers. obs.).

Cardamine concatenata (Michx.) Schwarz (*Dentaria concatenata* Michx.; *D. laciniata* Muhl. ex Willd.; *C. laciniata* (Muhl. ex Willd.) A. Wood (1870), non Steudel (1840), non F. Mueller (1855); *D. laciniata* vars. *alterna* Farw., *coalescens* Fern., *integra* (O. E. Schulz) Fern., *lasiocarpa* O. E. Schulz, *latifolia* Farw., *opposita* Farw.; *D. laciniata* f. *albiflora* Louis-Marie, f. *hexifolia* Wolden; *D. anomala* Eames, *pro parte*), pepperroot, is distributed in all the states east of the 95th meridian. It is uncommon in the eastern parts of Texas, Oklahoma, Kansas, and Nebraska and is sporadic in all of the Southeastern States except

FIGURE 2. **Cardamine.** a, *C. dissecta,* plant, × ½. b–d, *C. concatenata:* b, rhizome and rhizomal leaf, × ½; c, cauline leaf, × ½; d, trichomes of leaf margin, × 15. e, f, *C. angustata:* e, rhizome and rhizomal leaf, × ½; f, cauline leaf, × ½. g, *C. Longii,* plant,

Arkansas, Tennessee, and North Carolina, where it is abundant. In Canada it is restricted to southeastern Ontario and adjacent southern Quebec. *Cardamine concatenata* is easily distinguished by its moniliform rhizomes readily separable into fusiform, fleshy segments, its three (rarely two or more than three) approximate, three-foliolate, sharply toothed to incised (rarely subentire) cauline leaves, its usually hirsute inflorescence rachis, and its nonappressed, leaf-margin trichomes 0.2–0.3 mm long. All infraspecific taxa previously recognized in *Cardamine concatenata* have no geographic continuity, and all are based on minor differences that can be encountered within any sizeable population. The species is highly variable in the number and arrangement of its cauline leaves and in the width and margin of its leaflets.

Cardamine angustata O. E. Schulz (*Dentaria heterophylla* Nutt.; *C. heterophylla* (Nutt.) A. Wood (1870), non Host (1797), Lapeyr (1813), Bory (1820), Hooker (1835), (Forster) O. E. Schulz (1903), Cheo & Fang (1980); *C. angustata* var. *ouachitana* E. B. Smith) is distributed from Indiana south to northeastern Mississippi, east to South Carolina, and north to New Jersey. It is rare in South Carolina (Darlington and McCormick counties), Mississippi (Tishomingo County), and Arkansas (Howard, Montgomery, Polk, Pulaski counties) and has not yet been found in either Florida or Louisiana. Varietas *ouachitana* is said to differ from var. *angustata* in having glabrous instead of pubescent leaf margins (Smith, 1982). However, Harriman (1965) observed both glabrous and variously pubescent leaves in *C. angustata* (as *D. heterophylla*). Because of the continuous variation in the density of leaf-margin trichomes, var. *ouachitana* does not merit recognition. *Cardamine angustata* is recognized by its constricted rhizomes that are readily separable into segments, its rhizomal leaves that are very different morphologically and much broader than the cauline ones, and its leaf trichomes to 0.1 mm long (FIGURE 2e, f).

The final species is *Cardamine dissecta* (Leavenw.) Al-Shehbaz (*Dentaria dissecta* Leavenw.; *D. multifida* Muhl. ex Ell.; *C. multifida* (Muhl. ex Ell.) A. Wood, non Pursh; *C. laciniata* var. *multifida* (Muhl. ex Ell.) J. F. James; *D. laciniata* var. *multifida* (Muhl. ex Ell.) Watson & Coulter; *D. heterophylla* var. *multifida* (Muhl. ex Ell.) Ahles; *D. furcata* Small). It is distributed in Ohio, Indiana, Kentucky, Tennessee, North Carolina, Georgia, and Alabama (see Al-Shehbaz (1988) for further details). It can be recognized easily by its completely glabrous parts, its similar rhizomal and cauline leaves that are finely dissected into filiform to narrowly linear segments, and its moniliform rhizomes that readily separate into segments (FIGURE 2a). Harriman (1965) indicated that *C. angustata, C. concatenata,* and *C. dissecta* (as dentarias) are all self-compatible and have protogynous flowers with extrorse median stamens.

The four eastern North American "dentarias" have highly specialized cotyledons and seedlings. Both *Cardamine diphylla* and *C. concatenata,* as well as their putative hybrid *C.* ×*maxima* (Nutt.) A. Wood, have incumbent cot-

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× ½. h, *C. clematitis,* cauline leaf, × ½. i, *C. flagellifera,* cauline leaf, × ½. j–l, *C. diphylla:* j, rhizome and rhizomal leaf, × ½; k, cauline leaf, × ½; l, trichomes of leaf margin, × 30.

yledons strongly unequal in size. The larger cotyledon partially to completely enfolds the smaller one. When the seed germinates, the larger cotyledon emerges from the ground while the smaller one remains hypogeal within the seed coat (Harriman, 1965). In *C. angustata* and *C. dissecta* the cotyledons are accumbent, subequal, and similar to each other in shape. Seed germination in these two species is hypogeal, as is that of the European *C. pinnata* (Lam.) R. Br. (reported by Schulz, 1903). Hypogeal germination in the Cruciferae is apparently restricted to only a few species of *Cardamine.* In all these North American species the epicotyl enlarges in size and develops into a small rhizome that produces adventitious roots during the degeneration of the primary root.

Cardamine differs from the related *Rorippa* in having flat, elastically dehisced, spirally coiled valves, a narrowly winged replum, and uniseriately arranged seeds. *Rorippa* has convex, neither elastically dehisced nor spirally coiled valves, a wingless replum, and usually biseriately arranged seeds. Many species of *Rorippa* have yellow flowers and/or globose, oval to oblong fruits, neither of which is found in any species of *Cardamine. Loxostemon* has fruits similar to those of *Cardamine* but differs in having broadly winged filaments.

The weedy species of *Cardamine* are often autogamous annuals with small flowers and reduced petals. Self-incompatibility is widespread in the genus and has been studied in some detail in *C. pratensis* (Bateman). Protogyny occurs in many species, including *C. flagellifera* and *C. rotundifolia* (pers. obs.), as well as *C. rhomboidea* and *C. Douglassii* (Hart & Eshbaugh). Species of the *C. pratensis* complex are viviparous, capable under moist conditions of producing plantlets on the upper surface of the leaf lobes. The plantlets are derived from adventitious buds that originate exogenously from the hypodermis at the branching of the main veins. *Cardamine bulbifera* (L.) Crantz reproduces primarily by bulbils that are formed in the axils of the upper cauline leaves. The South American *C. chenopodiifolia* Pers. produces both normal flowers on terminal inflorescences and cleistogamous, subterranean, solitary flowers on peduncles that originate from the base of the plant. The latter flowers are apetalous and have a closed calyx, a reduced number of ovules and stamens, and a smaller amount of pollen. They produce indehiscent, one- to three-seeded fruits, while the aerial flowers form dehiscent, many-seeded ones.

Montgomery (1955) reported that the embryo sacs of some species of *Cardamine* (as *Dentaria diphylla, D. laciniata,* and *D. maxima* Nutt.) abort and die shortly after reaching the eight-celled stage. He concluded that these taxa form a sexually sterile polyploid series, members of which reproduce almost exclusively by rhizomes. Braun, however, discovering that *C. concatenata* (as *D. laciniata*) produces viable seeds in Ohio, questioned Montgomery's conclusion about the predominance of apomixis in this complex. Harriman (1965) reached a conclusion similar to Braun's and stated that *C. angustata, C. concatenata, C. diphylla,* and *C. dissecta* (as dentarias) are all sexual when seeds are produced. Spooner demonstrated that both megagametogenesis and megasporogenesis are normal in *C. concatenata* and concluded that the species is sexual. He suggested that sterility of some of the eastern North American dentarias has probably resulted from unbalanced genome combinations in hybrid populations or, alternatively, from the clonal growth of self-incompatible plants.

Chromosome numbers have been reported for 85 species, 87 percent of which are based on $x = 8$ (author's compilation). About 62 percent of the species are polyploid, and two, *Cardamine concatenata* and *C. diphylla* (both with $2n$ up to 256), have the highest known chromosome numbers in the Cruciferae. The lowest number in the genus ($2n = 12$) has been reported for the Caucasian *C. Seidlitziana* Albov (Goldblatt, 1984). It is evident that polyploidy has played a significant role in the evolution of *Cardamine.*

The eastern North American dentarias are probably the most cytologically variable of any species of Cruciferae. Harriman (1965) discovered that widely divergent chromosome numbers are found in plants of the same population, as well as within single root tips. In a population of *Cardamine diphylla* from Marion County, Tennessee, he observed $2n = 74$–83, 91–93, 96, 97, 100, 108, 113, 115, 130, 133, 134, 147, 148, 150, 151, 157–160, 167, 169, 171–250 (continuous series except 15 unobserved counts), 253, and 256. He also found $2n = 151$, 171, 173, 195, 196, 205, 207, 209–211, 224, and 247 in the same root tip. Harriman concluded that no fruitful generalizations can be made from root-tip chromosome counts of these dentarias and indicated that his attempts to study meiotic material were complicated by multivalent associations, lagging univalents, micronuclei, and high numbers and small sizes of chromosomes.

The *Cardamine pratensis* complex was thoroughly studied by Lövkvist (1956), who observed an exceptional range of chromosome levels from diploid ($2n = 16$) to dodecaploid ($2n = 96$), with many intermediate euploids and aneuploids. The "oscillation" in chromosome numbers depends on the occurrence of two basic numbers ($x = 7, 8$) and on the existence of hybrid swarms originating from parents with different numbers. Several authors have reported a correlation between water content of the soil and chromosome level of the plant. *Cardamine pratensis* sensu stricto ($2n < 56$) occupies drier habitats, while *C. palustris* (Wimmer & Grab.) Peterm. ($2n \geq 56$) is restricted to areas with high moisture content (e.g., bogs, marshes, springs, swamps). These taxa have been recognized either as distinct species (Jones, 1964; Lövkvist, 1956) or as subspecies or varieties of *C. pratensis* (Berg & Segal; Dale & Elkington; Fernald, 1950). Both species occur in eastern North America, but neither has been found in the Southeastern States.

Putative natural hybrids between *Cardamine rhomboidea* and *C. Douglassii* have been found. The species are easy to cross experimentally and are not genetically isolated. A reduction in hybrid fertility occurs when different chromosomal races of the two species are crossed (Hart & Eshbaugh). There is no effective isolating mechanism between the species, and although they generally flower two to four weeks apart, some overlapping occurs. The hybrids have flowering times intermediate between those of the parents.

Despite the lack of experimental evidence, many authors have suggested that natural interspecific hybridization must have occurred among the eastern North American dentarias. *Cardamine* ×*maxima* is intermediate between *C. concatenata* and *C. diphylla* in nearly all morphological characters, particularly those of the rhizomes and cauline leaves, as well as in its glucosinolate profiles (see below). It is a highly variable hybrid complex treated by Harriman (1965) as a distinct species. *Cardamine* ×*maxima* is almost always completely sterile and has never been found to produce seedlings. Fernald (1950) reported it from Tennessee, but Harriman (1965) did not cite any collections from that state. The latter author also recognized *Dentaria incisifolia* Eames ex Britton (*D. incisa* Eames, non Small), which is known from only one "population" in Fairfield County, Connecticut, as a distinct species said to differ from the other dentarias by the sessile "leaflets" of its cauline leaves. It is a completely sterile plant that can easily be accommodated in the extremely heteromorphic hybrid complex *C.* ×*maxima.* A putative hybrid swarm involving *C. angustata* and *C. dissecta* was found near the banks of Big Marrowbone Creek in Cheatham County, Tennessee (Harriman, 1965).

Jones (1975) listed several interspecific hybrids between various pairs of *Cardamine amara* L., *C. flexuosa, C. hirsuta,* and *C. pratensis.* Most of these hybrids have been recognized in Europe for many decades. Some (e.g., *C. flexuosa* × *C. pratensis* (*C.* ×*Haussknechtiana* O. E. Schulz)) are sterile perennials that reproduce only vegetatively. That this hybrid probably originated a few times independently is suggested by its occurrence in remotely separated areas and its failure to produce viable seeds.

The chemistry of *Cardamine* has not been studied adequately, and only a few species have been surveyed for fatty acids, flavonoids, and glucosinolates. Hart & Eshbaugh found 18 flavonoids in *C. rhomboidea* and *C. Douglassii.* The former is differentiated chemically into three races, of which one is indistinguishable from *C. Douglassii* in flavonoid profile. Of the six species analyzed for seed fatty acids, *C. bellidifolia* L. and *C. pratensis* have the highest content (36 percent) of linoleic acid known for any species of Cruciferae, while *C. graeca* L. contained the highest proportion (54 percent) of nervonic acid so far reported in any seed oil (Jart). The distribution of fatty acids may be chemotaxonomically useful in *Cardamine.*

About ten species of *Cardamine* have been surveyed for glucosinolates. Fresh parts of the western North American *C. cordifolia* A. Gray contain as many as nine compounds, of which one (2-butylglucosinolate) is the major constituent. The species is quite variable in its isothiocyanate-yielding glucosinolates, particularly in relation to plant part, season, and habitat (Rodman & Chew; Rodman & Louda, 1984, 1985; Louda & Rodman, 1983a, 1983b). Feeny & Rosenberry found similar variation in three dentarias and showed that the glucosinolate profile of *C.* ×*maxima* is intermediate between those of *C. diphylla* and of *C. concatenata.* Their findings support the hybrid origin of *C.* ×*maxima* from the last two species. All three contained various amounts of isopropyl, 2-butyl, and 2-methylbutyl glucosinolates, but *C. concatenata* had none or only traces of the last two compounds.

Despite the explosive dehiscence of fruits in *Cardamine,* seed dispersal may not exceed five feet (Kimata). Seeds of some of the weedy species (e.g., *C. hirsuta*) are mucilaginous when wet and can be transported by adhering to animals and equipment. The subterranean fruits of *C. chenopodiifolia* are not dispersed, and their seeds are buried effectively in the vicinity of the parent plant.

The fleshy underground parts of several species of *Cardamine* are eaten like radishes or used as a substitute for horseradish when grated and mixed with vinegar (Fernald & Kinsey). The young green parts of many species (e.g., *C. pensylvanica* and *C. rotundifolia*) are said to be an excellent substitute for watercress. Certain species are considered to have medicinal properties and are used in Asia as stimulants, diuretics, diaphoretics, and antidysenterics (Caius, Perry). Although a few species are cosmopolitan weeds, only *C. hirsuta* is a noxious garden and greenhouse plant.

REFERENCES:

Under family references in AL-SHEHBAZ (Jour. Arnold Arb. **65:** 343–373. 1984), see BAILLON; BENTHAM & HOOKER; BERGGREN; CAIUS; EASTERLY (1963); FERNALD; VON HAYEK; HEWSON; JART; KUMAR & TSUNODA; MARKGRAF; MURLEY; PERRY; RADFORD *et al.*; RICKETT; ROLLINS (1966, 1981); SCHULZ; SMALL; E. B. SMITH; and VAUGHAN & WHITEHOUSE.

Under tribal references see AL-SHEHBAZ (1977); APPELQVIST; BEAL; BOLKHOVSKIKH *et al.*; CHESTER; CLEWELL; COLE; CORBETT; CORRELL & CORRELL; DUNCAN & KARTESZ; ELLIS *et al.*; FASSETT; GATTINGER; GODFREY & WOOTEN; GOLDBLATT (1981, 1984, 1985); HEBEL; JONES (1974, 1975); KJAER; MACROBERTS; MATTHEWS *et al.*; MCKINNEY; MILLER *et al.*; MOHR; MOORE; NIELSEN *et al.*; PATMAN; PULLEN *et al.*; ROLLINS *et al.*; SHARP *et al.*; SMALL; THOMPSON; and VAN HORN.

AL-SHEHBAZ, I. A. *Cardamine dissecta,* a new combination replacing *Dentaria multifida* (Cruciferae). Jour. Arnold Arb. **69:** 81–84. 1988. [Evaluation of *Dentaria,* nomenclature and distribution of *C. dissecta.*]

BAEHNI, C. *Cardamine* and *Luxemburgia.* Notes de nomenclature. Candollea **7:** 279–282. 1937. [Comments on eight species of *Cardamine.*]

BANACH-POGAN, E. Karyological studies in species of *Dentaria* L. occurring in Poland. (In Polish; English summary.) Acta Soc. Bot. Polon. **23:** 375–382. 1954.

———. Further cytological studies in *Cardamine* L. (In Polish; English summary.) *Ibid.* **24:** 275–286. 1955. [*C. amara, C. flexuosa, C. hirsuta, C. impatiens, C. Opizii, C. trifolia.*]

BATEMAN, A. J. Self-incompatibility systems in angiosperms. III. Cruciferae. Heredity **9:** 53–68. 1955. [*C. pratensis,* 53–55.]

BEATUS, R. Die Selbsterilität von *Cardamine pratensis.* Jahrb. Wiss. Bot. **80:** 457–503. 1934. [A related paper in Ber. Deutsch. Bot. Ges. **47:** 189–199. 1929.]

BENOIT, P. M. Synthesised *Cardamine flexuosa* × *hirsuta.* (Abstr.) Proc. Bot. Soc. Brit. Isles **3:** 86. 1958. [The hybrid is completely sterile and produces aborted pollen.]

BERG, C. C. Cytotaxonomic studies in *Cardamine pratensis* L. in the Netherlands. Acta Bot. Neerl. **15:** 683–689. 1967. [Predominance of aneuploidy; tetraploids are treated as subsp. *pratensis,* higher ploidy levels as subsp. *palustris.*]

——— & S. SEGAL. De Pinksterbloem in Nederland. (English summary.) Gorteria **3:** 77–86. 1966. [*C. palustris, C. pratensis*; cytology, ecology, morphology.]

BISSELL, C. H. A new station for *Dentaria maxima.* Rhodora **5:** 168, 169. 1903. [Distributions of three species in Connecticut.]

BISWAS, K. Observations on Indian *Cardamine.* Trans. Proc. Bot. Soc. Edinburgh **33:** 416–430. 1943. [Treatment of 13 species.]

BRAUN, E. L. *Dentaria laciniata* from seed. Rhodora **59:** 267–269. 1957. [Seedling morphology; growth during the first year after germination.]

BUSCH, N. A. *Dentaria* and *Cardamine. In:* V. L. KOMAROV & N. A. BUSCH, eds., Fl. USSR **8:** 146–170. 1939. [English translation by R. LAVOOTT, **8:** 110–129. 1970.]

CHEPLICK, G. P. Differences between plants arising from aerial and subterranean seeds in the amphicarpic annual *Cardamine chenopodiifolia* (Cruciferae). Bull. Torrey Bot. Club **110:** 442–448. 1983. [Seeds produced in subterranean fruits are six times heavier than those from aerial fruits, and their seedlings grow faster.]

CHRIST, B. Entwicklungsgeschichtliche und physiologische Untersuchungen über die Selbsterilität von *Cardamine pratensis* L. Zeitschr. Bot. **47:** 88–112. 1959. [Site of incompatibility reaction; free amino acids and sugars in pollen and stigma.]

CRANTZ, H. J. N. Classis cruciformium emendata. 139 + 5 unnumbered index pp. *3 pls.* Leipzig. 1769. [*Cardamine* and *Dentaria* united, 126–132; 18 species recognized.]

CULLEN, J. *Cardamine. In:* P. H. DAVIS, ed., Fl. Turkey **1:** 438–444. 1965.

DALE, A., & T. T. ELKINGTON. Variation within *Cardamine pratensis* L. in England. Watsonia **10:** 1–17. 1974.

DELAVEAU, P. G., & F. FROMAGEOT. Recherches sur l'essence soufrée de la dentaire (*Dentaria pinnata* Lmk.) crucifères. (English summary.) Phytochemistry **2:** 237–240. 1963.

——— & A. KJAER.The mustard oils of *Dentaria pinnata* Lmk. Acta Chem. Scand. **17:** 2562, 2563. 1963.

DERSCH, G. Über das Vorkommen von diploidem Wiesenschaumkraut (*Cardamine pratensis* L.) in Mitteleuropa. (English summary.) Ber. Deutsch. Bot. Ges. **82:** 201–207. 1969. [Diploids ($2n = 16$) of the *C. pratensis* complex in France and Germany have one to four accessory chromosomes and are probably *C. nemorosa.*]

DETLING, L. E. A new *Cardamine* from northern Idaho. Madroño **3:** 176–178. 1935. [*C. Constancei.*]

———. The genus *Dentaria* in the Pacific States. Am. Jour. Bot. **23:** 570–576. 1936. [Differences between *Cardamine* and *Dentaria*; four species and 11 varieties recognized; key.]

———. The Pacific Coast species of *Cardamine. Ibid.* **24:** 70–76. 1937. [Taxonomy, relationships, and distributions of 14 species; key.]

DOYON, D. La distribution des espèces du genre *Dentaria* dans le Québec. (English summary.) Nat. Canad. **93:** 161–169. 1966. [*D. diphylla, D. laciniata, D. maxima*; distributions, ecology, maps.]

DUDLEY, T. R. The correct authority for *Cardamine clematitis* (Cruciferae). Rhodora **76:** 53–57. 1974.

EAMES, E. H. The dentarias of Connecticut. Rhodora **5:** 213–219. 1903. [*D. anomala, D. incisa,* spp. nov.; *D. diphylla, D. heterophylla, D. laciniata, D. maxima.*]

ELLIOT, G. F. S. *Cardamine pratensis* L. Rep. Bot. Soc. Exch. Club Brit. Isles **10:** 209–219. 1933. [Pollination, habitats; distribution of the genus.]

ELLIS, R. P. Taxonomy of the Arabideae (Cruciferae) with special reference to the genus *Cardamine.* Unpubl. Ph.D. dissertation, Univ. London. 1969.*

——— & B. M. G. JONES. The origin of *Cardamine flexuosa* with evidence from morphology and geographical distribution. Watsonia **7:** 92–103. 1969. [*C. flexuosa* originated by allopolyploidy from *C. hirsuta* and *C. impatiens*; distinguishing characters.]

——— & ———. *Cardamine*-pollen. *Ibid.* **8:** 45. 1970. [*C. flexuosa, C. hirsuta,* four other species.]

FEENY, P., & L. ROSENBERRY. Seasonal variation in the glucosinolate content of North American *Brassica nigra* and *Dentaria* species. Biochem. Syst. Ecol. **10:** 23–32. 1982. [*D. diphylla, D. laciniata, D. maxima*; glucosinolates support the hybrid origin of the last from the other two.]

FERNALD, M. L. A new *Cardamine* from southern Maine. Rhodora **19:** 91, 92. 1917. [*C. Longii.*]

———. Some variations of *Cardamine pratensis* in America. *Ibid.* **22:** 11–14. 1920. [Three indigenous varieties recognized.]

———. The American *Cardamine parviflora. Ibid.* **29:** 191, 192. 1927. [*C. parviflora* var. *arenicola*; synonymy, comparison with the European var. *parviflora.*]

——— & A. C. Kinsey. Edible wild plants of eastern North America. xii + 452 pp. New York and Evanston. 1943. (Revised by R. C. Rollins, 1958.) [*Cardamine, Dentaria,* 219–221.]

Gamm, R. Notes on amphicarpy—shown by the annual species *Cardamine chenopodiifolia* Pers. (Brassicaceae). (Abstr.) Acta Bot. Neerl. **32:** 346. 1983.

——— & F. Weberling. Sprossbürtige Wurzeln an den unterirdischen Fruchtstielen bei der amphikarpen Art *Cardamine chenopodiifolia* Pers. Flora **178:** 19–21. 1986. [Subterranean fruiting pedicels produce adventitious roots.]

Gleason, H. A. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Vol. **2.** iv + 655 pp. Lancaster, Pennsylvania. 1952. [*Cardamine, Dentaria,* 228–232.]

Greene, E. L. Studies in the Cruciferae.—I. 1. *Cardamine* and *Dentaria.* Pittonia **3:** 117–124. 1896. [Historic account; argument for recognition of both *Cardamine* and *Dentaria* as distinct genera; new combinations.]

Grimbach, P. Vergleichende Anatomie verschiedenartiger Früchte und Samen bei derselben Spezies. Bot. Jahrb. **51**(Beibl. 113): 1–52. 1913. [*C. chenopodiifolia,* 33–50, *figs. 22–31.*]

Habeler, E. Cytotaxonomie von *Cardamine amara* des Alpen-Ostrandes. Phyton Austria **10:** 161–205. 1963.

Harriman, N. A. Seed production and seedlings in the genus *Dentaria* (Cruciferae) in eastern North America. (Abstr.) Jour. Tenn. Acad. Sci. **38:** 60. 1963.

———. The genus *Dentaria* L. (Cruciferae) in eastern North America. vii + 210 pp. Unpubl. Ph.D. dissertation, Vanderbilt University, Nashville, Tennessee. 1965. [Relationship to *Cardamine,* comparative morphology, chromosome numbers, megasporogenesis, embryogeny, rhizome anatomy, self- and cross-incompatibility, putative interspecific hybridization, taxonomy and distributions of six species; *D. diphylla, D. heterophylla, D. incisifolia, D. laciniata, D. maxima, D. multifida.*]

Hart, T. W., & W. H. Eshbaugh. The biosystematics of *Cardamine bulbosa* (Muhl.) B.S.P. and *C. Douglassii* Britt. Rhodora **78:** 329–419. 1976. [Flavonoid chemistry, chromosome numbers, experimental hybridization, phenology, pollination, ecology, comparative morphology.]

Henry, M., & J.-L. Guignard. La régénération de plantes entières à partir de culture de cellules *in vitro* chez *Cheiranthus Cheiri* L. et *Cardamine pratensis* L. (Crucifères). Bull. Soc. Bot. France **126:** 143–147. 1979. [Callus formation, growth, and plant regeneration from hypocotyl and stem.]

Hill, P. L., Jr., & D. K. Evans. Taxonomy of the genus *Dentaria* (Cruciferae) in southern West Virginia. (Abstr.) Proc. West Virginia Acad. Sci. **51:** 6. 1979. [*D. diphylla, D. heterophylla, D. laciniata.*]

Hitchcock, C. L., A. Cronquist, M. Ownbey, & J. W. Thompson. Vascular plants of the Pacific Northwest. Part 2. 597 pp. Seattle. 1964. [*Cardamine,* 465–474.]

Howard, H. W. Chromosome number of *Cardamine pratensis.* Nature **161:** 277. 1948. [$n = 28$.]

———. The so-called chromosome-races of *Cardamine pratensis* and *Nasturtium officinale. Ibid.* **168:** 477, 478. 1951.

Hussein, F. Chromosome number of *Cardamine pratensis.* Nature **161:** 1015. 1948. [Cytogeography in England, $2n = 30$, 56.]

———. Chromosome races of *Cardamine pratensis* in the British Isles. P. 77 + *pls. 11–15 in* A. J. Wilmott, ed., British flowering plants and modern systematic methods. London. 1949. [$2n = 30$, 56.]

———. Chromosome races in *Cardamine pratensis* in the British Isles. Watsonia **3:** 170–174. 1955. [The northern and southern races have $2n = 56$ and 30, respectively.]

Iljinskij, A. P. On vegetative reproduction and phylogeny of some species of *Cardamine.*

(In Russian; English summary.) Bull. Jard. Bot. Prin. USSR **25:** 363–372. *map.* 1926. [*C. pratensis* complex; morphology, distributions, habitats, chromosome numbers.]

James, J. F. Remarks on *Dentaria* as a subgenus of *Cardamine.* Bot. Gaz. **8:** 206, 207. 1883. [*C. diphylla, C. heterophylla, C. laciniata* var. *multifida.*]

Jaspars-Schrader, T. W. Het onderscheid tussen *Cardamine flexuosa* With. en *C. hirsuta* L. (English summary.) Gorteria **10:** 213–219. 1982. [Differences between the two species.]

Jones, B. M. G. *Cardamine. In:* T. G. Tutin *et al.*, eds., Fl. Europaea **1:** 285–289. 1964. [Thirty-six species in two subgenera.]

———. *Cardamine.* Pp. 147–149 *in* C. A. Stace, ed., Hybridization and the flora of the British Isles. London, New York, and San Francisco. 1975. [Eight interspecific hybrids of six species.]

Khatari, K. S. Application of the names *Cardamine acris, C. dentata, C. scutata,* and *C. trifida.* Feddes Repert. **97:** 279–283. 1986.

Kimata, M. Comparative studies on the reproductive systems of *Cardamine flexuosa, C. impatiens, C. scutata,* and *C. lyrata,* Cruciferae. Bot. Mag. Tokyo **96:** 299–312. 1983. [Pollination, seed production, dispersal, germination, vegetative reproduction.]

Kral, R. Observations on the flora of the southeastern United States with special reference to northern Louisiana. Sida **2:** 395–408. 1966. [*C. concatenata* (as *Dentaria laciniata*) in Louisiana and Texas, 405, 406.]

———. Some notes on the flora of the Southern States, particularly Alabama and middle Tennessee. Rhodora **75:** 366–410. 1973. [*C. Douglassii,* new to Alabama, from four counties, 338.]

Landolt, E., & K. Urbanska-Worytkiewicz. Zytotaxonomische Untersuchungen an *Cardamine pratensis* L. s.l. im Bereich der Schweizer Alpen und des Jura. Ber. Deutsch. Bot. Ges. **84:** 683–690. 1972.

Lawrence, W. J. C. The chromosome constitution of *Cardamine pratensis* and *Verbascum phoeniceum.* Genetica **13:** 183–208. 1931. [*C. amara, C. asarifolia, C. pratensis.*]

Lebègue, A. Le proembryon de *Cardamine pratensis* L. Le suspenseur et la différenciation de l'hypophyse. Bull. Soc. Bot. France **96:** 205, 206. 1949.

Leopold, W. Beiträge zur Kenntnis der Gattung *Cardamine* mit besonderer Berücksichtigung der Hybridenfrage in der Sektion *Dentaria.* Denkschr. Akad. Wiss. Wien Math.-Naturw. **101:** 325–360. *pl.* 1928. [Morphology, anatomy, geography; several European species; *C. concatenata* (as *laciniata*).]

Louda, S. M., & J. E. Rodman. Ecological patterns in the glucosinolate content of a native mustard, *Cardamine cordifolia,* in the Rocky Mountains. Jour. Chem. Ecol. **9:** 397–422. 1983a. [Concentrations and distributions of nine glucosinolates in relation to plant part, leaf position and weight, phenology, habitat, and elevation; plant consumption by two insect herbivores.]

——— & ———. Concentration of glucosinolates in relation to habitat and insect herbivory for the native crucifer *Cardamine cordifolia.* Biochem. Syst. Ecol. **11:** 199–207. 1983b.

Louis-Marie, P. Le problème de nos dentaires hybrides. Revue Oka **14:** 155–162. 1940. [*Dentaria maxima.*]

Lövkvist, B. Chromosome studies in *Cardamine.* Hereditas **33:** 421, 422. 1947. [*C. pratensis* complex; correlation between higher chromosome numbers of plants and habitats with higher water content in soil.]

———. The *Cardamine pratensis* complex—outlines of its cytogenetics and taxonomy. Symb. Bot. Upsal. **14**(2): 1–131. *maps 1–16.* 1956. [Chromosome numbers, comparative morphology, reproductive biology, ecology, natural and artificial interspecific hybridization, speciation, taxonomy of seven species; key, distributions, descriptions.]

———. Experimental studies in *Cardamine amara.* Bot. Not. **110:** 423–441. 1957. [Chromosome numbers, induced polyploidy, interspecific crosses.]

LOWE, E. N. Plants of Mississippi. Mississippi State Geol. Surv. Bull. **17.** 292 pp. 1921. [*Cardamine, Dentaria,* 153, 154.]

MARCHAL, M. Ontogénie des bourgeons épiphylles de la *Cardamine.* (English summary.) Bull. Soc. Bot. France **115:** 31–43. 1968. [*C. pratensis*; morphology and anatomy of adventitious buds on leaf blades.]

MARHOLD, K. Karyotaxonomical notes of *Cardamine pratensis* agg. in Slovakia. (In Czech; English summary.) Biologia Bratislava **39:** 905–909. 1984. [*C. dentata, C. Matthioli, C. pratensis.*]

MCWILLIAM, A. Observations on occurrence and range of three species of *Dentaria* (Cruciferae) in the Ouachita Mountains. Proc. Ark. Acad. Sci. **20:** 22–24. 1966. [*D. heterophylla, D. laciniata, D. multifida.*]

MIKOLAJCZAK, K. L., C. R. SMITH, JR., & I. A. WOLFF. Dihydroxy fatty acids in *Cardamine impatiens* seed oil. Jour. Am. Oil Chem. Soc. **42:** 939–941. 1965.

———, ———, & ———. Glyceride structure of *Cardamine impatiens* L. seed oil. Lipids **3:** 215–220. 1968. [A related paper in *ibid.* **1:** 289, 290. 1966.]

MONACHINO, J. *Cardamine flagellifera* in West Virginia. Castanea **24:** 56, 57. 1959. [Distribution in Georgia, North and South Carolina, and West Virginia.]

MONTGOMERY, F. H. Preliminary studies in the genus *Dentaria* in eastern North America. Rhodora **57:** 161–173. 1955. [*D. diphylla, D. heterophylla, D. laciniata, D. maxima, D. multifida*; distributions, chromosome numbers, breeding systems, key.]

———. *Dentaria* in Indiana and Ohio. *Ibid.* **59:** 179, 180. 1957. [*D. diphylla, D. heterophylla, D. laciniata, D. multifida.*]

MULLIGAN, G. A. Chromosome numbers of the family Cruciferae. II. Canad. Jour. Bot. **43:** 657–668. 1965. [Ten species of *Cardamine.*]

OVERBECK, F. Über den Mechanismus der Samenausschleuderung von *Cardamine impatiens* L. Ber. Deutsch. Bot. Ges. **43:** 469–475. 1925. [Fruit dehiscence, seed dispersal, anatomy of valve.]

PETTY, R. O., & L. D. ESCOBAR. Variaciones fenotípicas en poblaciones de *Dentaria laciniata.* Actualid. Biol. **2:** 82–92. 1973. [Variations among three populations in Indiana.]

PIERIK, R. L. M. Effect of light and temperature on flowering in *Cardamine pratensis* L. Zeitschr. Pflanzenphysiol. **56:** 141–152. 1967.

PRITCHARD, G. G. Experimental taxonomic studies on species of *Cardamine* Linn. in New Zealand. Trans. Roy. Soc. New Zealand **85:** 75–89. 1957. [*C. bilobata, C. corymbosa, C. debilis, C. flexuosa, C. hirsuta*; chromosome numbers, descriptions, distributions, interspecific crosses.]

RODMAN, J. E., & F. S. CHEW. Phytochemical correlates of herbivory in a community of native and naturalized Cruciferae. Biochem. Syst. Ecol. **8:** 43–50. 1980. [*C. cordifolia.*]

——— & S. M. LOUDA. Phenology of glucosinolate concentrations in roots, stems and leaves of *Cardamine cordifolia.* Biochem. Syst. Ecol. **12:** 37–46. 1984. [Variability in glucosinolate content in relation to site, season, and plant part.]

——— & ———. Seasonal flux of isothiocyanate-yielding glucosinolates in roots, stems and leaves of *Cardamine cordifolia. Ibid.* **13:** 405–412. 1985. [Concentrations of glucosinolates declined seasonally in stems and cauline leaves but not in tubers, roots, and basal leaves.]

ROLLINS, R. C. A new *Cardamine* from North Carolina. Castanea **5:** 87, 88. 1940. [*C. micranthera,* sp. nov.; relationship to *C. rotundifolia.*]

———. *Cardamine digitata* Richardson (Cruciferae). Rhodora **54:** 260. 1952. [Nomenclature.]

ROONEY, S. C. Note on the first station of *Dentaria laciniata* Muhl. (Brassicaceae) reported from Maine. Rhodora **86:** 233, 234. 1984.

ROTH, I. Fruits of angiosperms. Encycl. Pl. Anat. **10**(1). xvi + 675 pp. Berlin and Stuttgart. 1977. [*Cardamine,* 184, 597, 598.]

ST. JOHN, H. Revision of *Cardamine* and related Cruciferae in Hawaii, and *Nasturtium* in Polynesia. Occas. Pap. Bishop Mus. **18:** 77–93. 1945.

SALISBURY, E. Weeds & aliens. *Frontisp.* + 384 pp. London. 1961. [*C. hirsuta,* ballistic dehiscence of fruits, seed dispersal, 108–110.]

———. The reproduction of *Cardamine pratensis* L. and *Cardamine palustris* Peterman particularly in relation to their specialized foliar vivipary, and its deflexion of the constraints of natural selection. Proc. Roy. Soc. Biol. London, B. **163:** 321–342. 1965.

SCHEMSKE, D. W., M. F. WILLSON, M. N. MELAMPY, L. J. MILLER, L. VERNER, K. M. SCHEMSKE, & L. B. BEST. Flowering ecology of some spring woodland herbs. Ecology **59:** 351–366. 1978. [*C. concatenata* (as *Dentaria laciniata*); protogyny, self-compatibility, pollinators, seed set, phenology.]

SCHNEDLER, W. Rosettenblätter der kleinen *Cardamine*-Arten. Gött. Flor. Rundbr. **12:** 65, 66. 1978. [*C. flexuosa, C. hirsuta, C. impatiens*; key.]

SCHULZ, O. E. Monographie der Gattung *Cardamine.* Bot. Jahrb. **32:** 280–623. *pls. 7–10.* 1903. [Comparative morphology, ecology, relationship and differences between *Cardamine* and *Rorippa* (as *Nasturtium*), evaluation of *Dentaria,* sectional classification, taxonomy of 116 species in 12 sections.]

SCHWARZ, O. Namensänderungen bei *Cardamine* subgen. *Dentaria.* Repert. Sp. Nov. **46:** 188. 1939. [Nomenclature of *C. concatenata* and *C. heterophylla.*]

SCHWARZENBACH, F. Untersuchungen über die Sterilität von *Cardamine bulbifera* (L.) Crantz unter der Annahme eines hybriden Ursprungs dieser Art. Flora **115:** 393–514. *pls. 11–13.* 1922. [The European members of subg. *Dentaria*; cytology, morphology, ecology, distributions, flower and fruit formation, interspecific hybridization. *C. bulbifera*; fertility and sterility, hybrid origin, chromosome numbers.]

SHARP, A. J., & A. BAKER. First and interesting reports of flowering plants in Tennessee. Castanea **29:** 178–185. 1964. [*C. flagellifera* in Blount, Polk, and Sevier counties, 180.]

SHETLER, S. G. Application of the names *Cardamine digitata, Dentaria pentaphylla,* and *D. heptaphylla.* Taxon **10:** 264–267. 1961.

SJÖSTEDT, B. Revision of the genus *Cardamine* L. (Cruciferae) in South and Central America. Bot. Not. **128:** 8–19. 1975. [Thirty-seven species reduced to only five; key, synonymy, descriptions, distributions.]

SMITH, E. B. A new variety of *Cardamine angustata* (Cruciferae) from the Ouachita Mountains of Arkansas. Brittonia **34:** 376–380. 1982. [Plants with glabrous leaves described as var. *ouachitana.*]

SOUCHON, C., & R. TOMASSONE. Caractérisation de trois formes de *Cardamine pratensis* L. en vue d'une étude écophysiologique comparée. II.—Étude taxonomique et biométrique. (English summary.) Rev. Gén. Bot. **78:** 387–405. 1971. [Part I in *ibid.* 373–386.]

SPASSKAYA, N. A. Synopsis of the system of genus *Cardamine* L. for the European part of the Soviet Union. Vestn. Biol. Leningrad Univ. **15**(3): 40–48. 1978.*

———. Chromosome numbers of species of the genus *Cardamine* L. (Brassicaceae) from the European part of the USSR. (In Russian; English summary.) Bot. Zhur. **64:** 1099, 1110. 1979. [Thirteen species; polyploidy, karyological variation.]

SPOONER, D. M. Reproductive features of *Dentaria laciniata* and *D. diphylla* (Cruciferae), and the implications in the taxonomy of the eastern North American *Dentaria* complex. Am. Jour. Bot. **71:** 999–1005. 1984. [Micro- and megasporogenesis, embryogeny, test for agamospermy, seed germination, sexuality.]

STEYERMARK, J. A. Flora of Missouri. lxxxiii + 1725 pp. Ames, Iowa. [1963.] [*Cardamine, Dentaria,* 748–751.]

STUCKEY, R. L. Characteristics and distribution of the spring cresses, *Cardamine bulbosa* and *C. Douglassii,* in Michigan. Mich. Bot. **1:** 27–34. 1962. [Distinguishing characters, nomenclatural history, synonymy, varieties, distributions, hybridization.]

———. *Thlaspi tuberosum* Nutt., a taxonomic synonym of *Cardamine Douglassii* Britt. (Cruciferae). Rhodora **69:** 460–465. 1967.

Suksdorf, W. *Cardamine oligosperma* and its near allies. Rhodora **20:** 197–199. 1918. [See Torrey.]

Sutter, R. D., L. Mansberg, & J. Moore. Endangered, threatened, and rare plant species of North Carolina. ASB Bull. **30:** 153–163. 1983. [*C. angustata* var. *multifida, C. Douglassii, C. Longii, C. micranthera,* and *C. rotundifolia* are rare, 158.]

Thurling, N. Population differentiation in Australian *Cardamine.* I. Variation in leaf characters. Austral. Jour. Bot. **14:** 167–178. 1966. [Part II, response to variations in temperature and light intensity, *ibid.* 179–188; part III, variation in germination response, *ibid.* 189–194; part IV, variation in flowering response, *ibid.* **15:** 459–466. 1967.]

———. A cytotaxonomic study of Australian *Cardamine. Ibid.* **16:** 515–523. 1968. [*C. flexuosa, C. hirsuta*; chromosome numbers, cross-compatibility relationships, evolution, and taxonomic implications of four other species not provided with binomials.]

Torrey, G. S. The varieties of *Cardamine oligosperma.* Rhodora **17:** 156–158. 1915. [Pacific North American taxa; see Suksdorf.]

Urbanska-Worytkiewicz, K. Reproduction in natural triploid hybrids ($2n = 24$) between *Cardamine rivularis* Schur and *C. amara* L. Ber. Geobot. Inst. Tech. Rübel **44:** 52–85. 1977a.

———. An autoallohexaploid in *Cardamine* L., new to the Swiss flora. *Ibid.* 86–103. 1977b. [*C. Schulzii,* sp. nov., derived from *C. amara* × *C. rivularis.*]

——— & E. Landolt. Remarques sur l'aneuploïde chez *Cardamine pratensis* L. s. l. (English summary.) Ber. Geobot. Inst. Tech. Rübel **42:** 31–41. 1974a. [*C. nemorosa, C. pratensis*; polysomy, aneuploidy, karyotypes, role of hybridization.]

——— & ———. Biosystematic investigations in *Cardamine pratensis* L. s. l. I. Diploid taxa from central Europe and their fertility relationships. *Ibid.* 42–139. 1974b. [*C. granulosa, C. Matthioli, C. nemorosa, C. pratensis, C. rivularis, C. udicola*; morphology, key, distributions, ecology, chromosome numbers, karyotypes, breeding systems, interspecific hybridization, reproductive isolation.]

Vandendries, R. Contribution à l'étude du développement de l'ovule dans les crucifères. II. L'archésporium dans le genre *Cardamine.* Cellule **28:** 215–225. *pl.* 1912. [*C. amara, C. hirsuta, C. impatiens, C. sylvatica.*]

Villani, A. Contributo allo studio dei nettarii del genere *Cardamine* (Tourn.) L. Nuovo Giorn. Bot. Ital. II. **21:** 247–263. *pl. 4.* 1914.

Vogt, R. Notes on seedlings. I. *Cardamine Douglassii.* Am. Midl. Nat. **3:** 287, 288. *pls. 4–8.* 1914. [Tuberous part derived from epicotyl.]

Voss, E. G. Michigan flora. Part 2. xix + 724 pp. Ann Arbor. 1985. [*Dentaria,* 277–280; *Cardamine,* 282–286.]

Vyvey, R., & H. Stieperaere. A numerical analysis of some diploid and tetraploid *Cardamine pratensis* L. (s. l.) populations from Belgium and northern France. Bull. Soc. Bot. Belg. **117:** 341–350. 1984.*

Weber, A. Stipularbildungen bei *Dentaria* und ihr Wert für die morphologische Deutung der Speicherschuppen als Phyllodein. (English summary.) Österr. Bot. Zeitschr. **121:** 107–119. 1973. [*D. bipinnata, D. bulbifera, D. enneaphyllos, D. pentaphyllos*; rhizomal scales interpreted as phyllodial scales, not stipules.]

White, P. S., & B. E. Wofford. Rare native Tennessee vascular plants in the flora of Great Smoky Mountain National Park. Jour. Tenn. Acad. Sci. **59:** 61–64. 1984. [*C. clematitis* in Carter and Sevier counties; *C. flagellifera* in Blount, Knox, Polk, and Sevier counties.]

Wolden, B. O. A six-leaved *Dentaria.* Am. Bot. **23:** 18, 19. 1917. [*D. laciniata* f. *hexifolia.*]

28. **Barbarea** R. Brown in Aiton, Hortus Kew. ed. 2. **4:** 109. 1812, nom. cons.[7]

Biennial or perennial [very rarely annual] herbs, glabrous or sparsely pubescent with unbranched trichomes. Stems erect, angular, usually branched. Basal leaves rosulate, petiolate, lyrately pinnatifid or pinnatisect [or undivided], with 1–10 pairs of lateral lobes, terminal lobe always much larger than the lateral ones. Cauline leaves sessile, usually amplexicaul or auriculate, entire or dentate to pinnatifid, glabrous or ciliate at base. Inflorescence a densely flowered, ebracteate [or bracteate], corymbose raceme, greatly [or not] elongated in fruit; base of flowering pedicels with a minute gland on each side; fruiting pedicels erect and appressed to rachis or spreading, stout and nearly as thick as the fruit or slender, terete or angled. Sepals oblong to linear, ascending [erect or spreading], glabrous [or with subapical trichomes]; outer pair usually cucullate at apex, not saccate at base; inner pair not cucullate, slightly saccate. Petals bright [to pale] yellow, spatulate to oblanceolate, short clawed, about twice as long as [or only slightly longer than] sepals. Nectar glands 4, distinct; lateral pair horseshoe shaped, open to the outside; median pair toothlike or rod shaped. Stamens 6, tetradynamous; filaments free, not appendaged; anthers oblong. Fruits dehiscent, linear, terete to 4-angled or flattened parallel to the septum, torulose to smooth, straight to arcuate, erect or ascending to divaricate; valves with a prominent midnerve and conspicuous or obscure lateral nerves, rarely carinate, glabrous [or very rarely pubescent]; gynophore stout, to 1 mm long; styles persistent, short or long, slender to stout; stigmas capitate, slightly 2-lobed. Seeds dark brown, prominently [or slightly] reticulate, uniseriately arranged in each locule, usually neither winged nor marginate, nonmucilaginous when wet; cotyledons accumbent. Base chromosome number 8. (Including *Campe* Dulac.) TYPE SPECIES: *Erysimum Barbarea* L. = *B. vulgaris* R. Br.; see ICBN, p. 350. 1983. (Name commemorates St. Barbara, of the fourth century. The seeds of *B. verna* (Miller) Ascherson, a plant called herb of St. Barbara in the Middle Ages, were sown in western Europe in early December near St. Barbara's day. A few authors maintain that the name is derived from the fact that species of *Barbarea* were the only plants available for food on St. Barbara's Day.)—WINTER CRESS, SCURVY GRASS, ROCKET, UPLAND CRESS, CORN MUSTARD (Small).

A well-defined but taxonomically difficult genus of about 20 species distributed primarily in Europe and Asia, particularly the Balkan peninsula (ten species, six endemic), Turkey (ten species, five endemic), and the Caucasus (six species, two endemic). The native range of *Barbarea orthoceras* Ledeb. (*B. americana* Rydb., *B. planisiliqua* C. A. Meyer) includes central and eastern Asia and North America (Alaska to Baja California, east into the Mountain States, Michigan, New York, New Hampshire, and Maine, north throughout most of Canada). Hewson recognized *B. australis* J. D. Hooker and *B. Grayi* Hewson as indigenous to Tasmania and adjacent southeastern Australia, respectively. Both are disjunct from the rest of *Barbarea* and are anomalous in

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[7] For conservation of the generic name, see the papers of Eichler, Fuchs, McVaugh, and Rauschert.

that they are annuals with tuberculate, marginate or narrowly winged seeds. It is doubtful whether they should be retained in this genus. The majority of species grow in wet habitats, but at least four are widely distributed weeds of roadsides, fallow and cultivated fields, pastures, waste places, and open woods. The genus is represented in the southeastern United States by two naturalized weeds.

Barbarea vulgaris R. Br. (*Erysimum Barbarea* L., *Sisymbrium Barbarea* (L.) Crantz, *Barbarea Barbarea* (L.) MacM., *Campe Barbarea* (L.) W. F. Wight, *B. taurica* DC., *E. arcuatum* Opiz ex Presl, *B. arcuata* (Opiz ex Presl) Reichenb., *B. vulgaris* var. *arcuata* (Opiz ex Presl) Fries), common winter cress, yellow rocket, bitter cress, rock cress, $2n = 16$, is a Eurasian weed that is naturalized throughout most of North America. It has been reported from all of the Southeastern States except Mississippi and Louisiana, where it is likely to be found. It is one of the most variable species of *Barbarea,* and on the basis of length and orientation of both fruits and fruiting pedicels, a few authors (e.g., Fernald, 1943; Jackson) have recognized several varieties and forms. These characters show continuous variation, and it is highly doubtful that any of the infraspecific taxa of *B. vulgaris* merit recognition. Plants comparable to "vars." *vulgaris* (fruits straight, appressed to rachis) and *arcuata* (fruits spreading, usually arcuate), as well as a wide array of intermediates, grow in the Southeast and throughout the native and naturalized ranges of the species.

Small (1903; 1933, family references) reported the Eurasian *Barbarea stricta* Andrz. from Florida, but it is very likely that his record was based on misidentified plants of *B. vulgaris.* According to Ball, both species have dentate uppermost cauline leaves, but the former has pubescent flower buds and fruiting styles 0.5–1.5 mm long, while the latter has glabrous buds and styles 2–3 mm long. I have not studied enough material of *B. stricta* to evaluate its variation in these characters, but in *B. orthoceras* glabrous or pubescent buds, appressed to spreading fruits and fruiting pedicels, and dentate to pinnatifid upper cauline leaves may be found within the same population. Both *B. stricta* and *B. orthoceras* are distinguished from *B. vulgaris* by their short, stout fruiting styles. *Barbarea orthoceras* is quite variable in North America, and as presently circumscribed, it can easily accommodate the earlier-published *B. stricta.* It is interesting that many earlier North American botanists had passed *B. orthoceras* as *B. stricta.* It is evident that the three species above need careful evaluation of their boundaries and their variation in leaves and fruits. Fernald (1909) recognized plants of *B. orthoceras* with spreading fruits as var. *dolichocarpa* Fern., but as indicated above, forms with appressed or spreading fruits completely intergrade within numerous populations.

Barbarea verna (Miller) Ascherson (*Erysimum vernum* Miller, *Campe verna* (Miller) Heller, *E. praecox* James Sm., *B. praecox* (James Sm.) R. Br.), early winter cress, land cress, scurvy grass, Belle Isle cress, $2n = 16$, is another Eurasian weed that is widely distributed in the United States and is naturalized in all of the Southeastern States. It is easily distinguished from *B. vulgaris* in having basal leaves with six to ten pairs of lateral lobes, pinnatisect uppermost cauline leaves, stout styles 0.5–1(–2) mm long, and ascending fruits 4.5–8 cm long. *Barbarea vulgaris* has basal leaves with three to five pairs of lateral lobes, dentate to entire uppermost cauline leaves, slender styles 1.5–3 mm long, and appressed to spreading fruits (0.7–)2–3 cm long.

The placement of *Barbarea* in the tribe Arabideae has been accepted by most students of the Cruciferae. The genus is usually associated with *Arabis, Cardamine,* and *Rorippa,* the core genera of the tribe. Von Hayek derived *Barbarea* directly from *Erysimum* L. and considered it to be ancestral to *Rorippa,* while Schulz placed it between the North American *Thelypodium* Endl. (as *Pleurophragma* Rydb.) and *Phoenicaulis* Nutt. ex Torrey & A. Gray. In my opinion, Von Hayek's association of *Barbarea* with *Rorippa,* but not with *Erysimum,* is more acceptable than Schulz's generic disposition. *Barbarea* is distinguished from other genera of the Arabideae by its yellow flowers, uniseriately arranged seeds, strongly nerved valves, and auriculate cauline leaves, as well as by the presence of a pair of glands at the base of each pedicel and by either the lack of indumentum or the presence of simple trichomes only.

As indicated by Fernald (1909, p. 134), species of *Barbarea* are "notoriously difficult of delimitation." Specimens should include mature fruits and basal leaves, and field notes should cover the variation of important diagnostic features, such as the length and orientation of fruits and fruiting pedicels, the number of lateral lobes of the basal leaves, and the margin of the uppermost cauline leaves. Several species are recognized on the basis of minor differences in characters the variation of which is poorly understood. Species boundaries are probably obscured by hybridization, but there is no documentation that this has actually taken place. Careful evaluation of species, particularly of the Caucasus region, Turkey, and the Balkan peninsula, is needed.

Little is known about the reproductive biology of the genus. Both *Barbarea verna* and *B. vulgaris* are self-compatible, and the latter and *B. orthoceras* are often protogynous (pers. obs.). Fertig (in MacDonald & Cavers) estimated that a medium-sized plant of *B. vulgaris* can produce more than 200,000 seeds. The species also reproduces asexually by the formation of adventitious buds from roots (Kott) or by the development of "cauline rosettes" in axils of the uppermost cauline leaves (MacDonald & Cavers; Rich). The latter phenomenon was observed in about one percent of the plants of a given population. If the "cauline rosettes" come in contact with the ground (due to bending of the stem), they may produce adventitious roots and may flower and fruit the next season after overwintering. Factors promoting the formation of "cauline rosettes" are unknown, but hormonal or physiological imbalances following injury have been suggested (Rich). Both *B. verna* and *B. vulgaris* have an obligate cold requirement for flowering.

Chromosome numbers are known for 12 species of *Barbarea,* and all counts except two for *B. vulgaris* indicate that $2n = 16$. Deviating counts of $2n = 18$ have been reported for plants from Czechoslovakia (Dvořák & Dadáková; Dvořák *et al.*). Neither polyploidy nor aneuploidy has played a major role in the evolution of the genus.

Although interspecific hybridization between pairs of closely related species of *Barbarea* has been suggested, none of the alleged cases has been verified experimentally. The putative hybrids *B. stricta* × *B. vulgaris* (*B.* ×*Schulziana*

Hausskn.) and *B. intermedia* Boreau × *B. vulgaris* (*B.* ×*Gradlii* J. Murr) have been recorded from Germany, Czechoslovakia, and Austria (Lange, Markgraf, Stace).

The five species of *Barbarea* that have been surveyed for glucosinolates contain high concentrations of 2-phenylethyl and/or 2-hydroxy-2-phenylethyl glucosinolates. Small amounts of 3-methylthiopropylglucosinolate are found in *B. vulgaris, B. plantaginea* DC., and *B. intermedia,* and traces of isopropylglucosinolate are present in the last and in *B. stricta* (Cole; Al-Shehbaz & Al-Shammary). The seeds of both *B. vulgaris* and *B. stricta* have been analyzed for fatty acids. They contain moderate amounts (21–26 percent) of oleic, linoleic, and erucic acids. Smaller amounts (16 percent) of the last acid were found in *B. orthoceras* (Goering *et al.*).

Barbarea verna and *B. vulgaris* are very similar in seed-coat anatomy. Both have a palisade layer composed of isodiametric cells with thickened radial and inner tangential walls, but cells of the latter species have prismatic crystals. The epidermis in both species has been said to be mucilaginous (Vaughan & Whitehouse), but no mucilage was observed in seeds of these or of several other species of *Barbarea* that I have examined.

Several species of *Barbarea* are cosmopolitan weeds that are among the earliest to flower in the spring. Both *B. verna* and *B. vulgaris* are cultivated in parts of Europe as potherbs and are said to have a flavor similar to that of watercress, *Rorippa Nasturtium-aquaticum. Barbarea vulgaris* was cultivated by the early Egyptians, Greeks, and Romans, and its leaves are eaten in Sweden as a substitute for kale. The plants are not bitter when young but become so as the season progresses. Leaves of older plants are edible only if cooked in two waters. The species is said to be a stimulant, an antiscorbutic, and a vulnerary (Caius), as well as a valuable honey plant in cold regions.

References:

Under family references in Al-Shehbaz (Jour. Arnold Arb. **65:** 343–373. 1984), see Baillon; Bentham & Hooker; Berggren; Britton & Brown; Busch; Caius; De Candolle (1821, 1824); Fernald; Goering *et al.*; Von Hayek; Hewson; Janchen; Knuth; Manton; Markgraf; Muenscher; Murley; Radford *et al.*; Rickett; Rollins (1981); Schulz; Small; E. B. Smith; and Vaughan & Whitehouse.

Under tribal references see Al-Shehbaz (1977); Al-Shehbaz & Al-Shammary; Appelqvist; Bolkhovskikh *et al.*; Cole; Corbett; Correll & Correll; Daxenbichler *et al.*; Duncan & Kartesz; Ellis *et al.*; Goldblatt (1981, 1984, 1985); Hebel; Jones (1975); Kjaer; Litchfield; MacRoberts; Matthews *et al.*; McKinney; Miller *et al.*; Moore; Sharp *et al.*; Small; Stace; and Thompson.

Ančev, M. E. *In:* Á. Löve, ed., Chromosome number reports LXXIII. Taxon **30:** 829–861. 1981. [*B. bracteosa,* $2n = 16$; *B. vulgaris,* $2n = 16$; 855.]

Andersson, I. Structural mosaics and inheritance of variegation in *Barbarea vulgaris.* Jour. Genet. **14:** 185–195. *pls. 3–8.* 1924.

Ball, P. W. *Barbarea. In:* T. G. Tutin *et al.,* eds., Fl. Europaea **1:** 281, 282. 1964.

Cayouette, J. Nouvelles stations du *Barbarea stricta* Andrz. au Québec. (English summary.) Nat. Canad. **111:** 207–209. 1984. [Differences among *B. orthoceras, B. stricta,* and *B. vulgaris.*]

Chaturvedi, S. N., & R. K. S. Rathore. Morphological studies in *Barbarea vulgaris*

R. Br. Jour. Indian Bot. Soc. **49:** 58–63. 1970. [Micro- and megasporogenesis, embryology, developmental anatomy of seed coat.]

Coode, M. J. E., & J. Cullen. *Barbarea. In:* P. H. Davis, ed., Fl. Turkey **1:** 433–438. 1965. [Ten species recognized.]

Dahlgren, K. V. O. Vererbungsversuche mit einer buntblättrigen *Barbarea vulgaris.* Hereditas **2:** 88–98. 1921.

Dvořák, F., & B. Dadáková. Chromosome counts and chromosome morphology of some selected species. Folia Geobot. Phytotax. **19:** 41–70. 1984. [*B. vulgaris* (as *B. arcuata*), 58; $2n = 18$.]

———, F. Grüll, K. Sutorý, & B. Dadáková. *In:* Á. Löve, ed., Chromosome number reports LXXIII. Taxon **30:** 829–861. 1981. [*B. stricta,* $2n = 16$; *B. vulgaris* (as *B. arcuata*), $2n = 18$; 844.]

Eichler, H. *Barbarea* or *Campe*? Taxon **12:** 262–264. 1963. [*Barbarea* sensu R. Brown was used by B. Ehrhart in 1753 and 1756; suggests that the generic name needs neither to be conserved nor to be replaced by *Campe*; see Fuchs, McVaugh, and Rauschert.]

Fernald, M. L. The North American species of *Barbarea.* Rhodora **11:** 134–141. 1909. [*B. orthoceras, B. planisiliqua, B. verna, B. vulgaris.*]

———. Our varieties of *Barbarea vulgaris. Ibid.* **45:** 304. 1943. [Four varieties and two forms recognized; key.]

Fuchs, H. P. *Barbarea* B. Ehrhart versus *Campe* Dulac. Taxon **14:** 99–103. 1965. [*Barbarea* R. Br. (1812) was rejected and *Campe* was accepted because the former was a later homonym of *Barbarea* of B. Ehrhart (1756), Scopoli (1760), and Agosti (1770); see Eichler, McVaugh, and Rauschert.]

Fursa, N. S., V. I. Litvinenko, & P. E. Krivenchuk. Flavonoids from *Armoracia rusticana* and *Barbarea arcuata.* (In Russian.) Khim. Prir. Soedin. **1969:** 320. 1969. [Isorhamnetin glucopyranoside and glucosyl glucoside in *B. vulgaris* (as *B. arcuata*).]

Ham, R. W. J. M. van der. *Barbarea intermedia* Bor. en *Barbarea verna* (Mill.) Aschers. in Nederland. (English summary.) Gorteria **11:** 36–39. 1982. [Distributions, key to species.]

Hedge, I. *Barbarea. In:* K. H. Rechinger, ed., Fl. Iranica **57:** 198–200. 1968.

Hintikka, T. J. Zur Kenntnis einer Blütenanomalie bei *Barbarea vulgaris* R. Br. Mem. Soc. Fauna Flora Fenn. **15:** 67–79. 1939.

Jackson, A. B. A study of *Barbarea vulgaris* R. Br. Jour. Bot. London **54:** 202–208. 1916. [Variation, nomenclature; five varieties recognized.]

——— & A. J. Wilmott. *Barbarea rivularis* in Britain. Jour. Bot. London **57:** 304–306. 1919. [*B. vulgaris.*]

Kjaer, A., & R. Gmelin. Isothiocyanates XXVIII. A new isothiocyanate glucoside (glucobarbarin) furnishing (-)-5-phenyl-2-oxazolinethione upon enzymic hydrolysis. Acta Chem. Scand. **11:** 906, 907. 1957. [*B. vulgaris.*]

Kott, S. A. Biology of the winter cress. (In Russian.) Bot. Zhur. **48:** 1648–1652. 1963. [*B. vulgaris*; asexual reproduction, weed control.]

Lange, T. Sveriges *Barbarea*-arter. Bot. Not. **1937:** 216–230. 1937. [Distributions of three species and two interspecific hybrids, key.]

MacDonald, M. A. Effects of environmental heterogeneity on the abundance of *Barbarea vulgaris* R. Br. Diss. Abstr. Int. **38:** 4042B. 1978.

——— & P. B. Cavers. Cauline rosettes—an asexual means of reproduction and dispersal occurring after seed formation in *Barbarea vulgaris* (yellow rocket). Canad. Jour. Bot. **52:** 913–918. *figs. 3–7.* 1974. [Rosettes produced in the axils of uppermost cauline leaves may develop adventitious roots if the rachis is bent to the ground; these may overwinter and produce flowers and fruits the next season.]

Mardalejschvili, T. K. New species of the genus *Barbarea* R. Br. (Brassicaceae) from the subnival belt of Svanetia range (western Georgia). (In Russian.) Bot. Zhur. **62:** 1299, 1300. 1977. [*B. Ketzkhovelii*, sp. nov.]

McVaugh, R. Report of the committee for Spermatophyta. Conservation of generic names, VIII. Taxon **17:** 85–87. 1968. [Proposal to conserve *Barbarea* R. Br. and reject the earlier-published *Barbarea* Scop. (= *Cardamine*) and the uninomial *Barbarea* B. Ehrh.; for approval of the proposal, see *ibid.* 450; see Eichler, Fuchs, and Rauschert.]

Mugnier, C. Caractéristiques de la vernalisation d'une plante vivace, le cresson de terre, *Barbarea praecox* R. Br. (English summary.) Bull. Soc. Bot. France **126:** 279–292. 1979. [*B. verna* (as *B. praecox*) has an absolute cold requirement for flowering.]

Mulligan, G. A. *Barbarea stricta* Andrz., a new introduction to Quebec. Nat. Canad. **105:** 297, 298. 1978. [Key to the native and naturalized species of *Barbarea* in North America.]

Polatschek, A. Chromosomenzahlen und Hinweise auf Systematik und Verbreitung von Brassicaceae-Arten aus Europa, Nordafrika, Asien und Australien. (English summary.) Phyton Austria **23:** 127–139. 1983. [*B. balcana, B. bosniaca, B. stricta, B. vulgaris,* 129, 130.]

Raimondo, F. M., M. Rossitto, & D. Ottonello. Numeri cromosomici per la flora Italiana: 967–976. Inform. Bot. Ital. **15:** 58–65. 1983. [*B. bracteosa, B. sicula,* 59–61; $2n = 16$.]

Rauschert, S. Ist *Barbarea* Ehrhart ein legitimer Gattungsname? Feddes Repert. **73:** 222–225. 1966. [No; *Campe* accepted and *Barbarea* R. Br. rejected, several new combinations; see Eichler, Fuchs, and McVaugh.]

Rich, T. C. G. Asexual reproduction of *Barbarea vulgaris* R. Br. in the British Isles. Watsonia **15:** 121, 122. 1984.

———. The genus *Barbarea* R. Br. (Cruciferae) in Britain and Ireland. *Ibid.* **16:** 389–396. 1987. [*B. intermedia, B. stricta, B. verna, B. vulgaris*; reproductive biology, key, descriptions.]

Rohweder, O. Über verlaubte Blüten von *Barbarea vulgaris* R. Br. und ihr morphologische Bedeuting. Flora **148:** 255–282. 1959. [Normal and anomalous development of flowers.]

Schreiber, M. M. Growth, development and perennial nature of yellow rocket. Weeds **10:** 91–95. 1962.* [*B. vulgaris.*]

——— & S. N. Fertig. The chemical composition of yellow rocket (*Barbarea vulgaris*). Agron. Jour. **47:** 104, 105. 1955. [Minerals, protein content, fiber, ash.]

Taylorson, R. B. Responsiveness of intact and scarified seeds of *Barbarea vulgaris* to gibberellic acid and changes in phytochrome. Physiol. Pl. **38:** 196–200. 1976. [A related paper in *ibid.* 201–207.]

Tilney-Bassett, R. A. E. Selection against variegated genotype in *Barbarea vulgaris.* Heredity **18:** 543–545. 1963. [Leaf variegation is controlled by a single recessive allele; reduced viability of variegated seeds, poor growth of variegated seedlings.]

Toole, E. H., & V. K. Toole. Notes on the germination of seeds of *Barbarea verna* and *Lepidium virginicum.* Proc. Int. Seed Testing Assoc. **12:** 32–38. 1940.*

Turrill, W. B. Thracian cress: a new salad plant. Gard. Chron. III. **108:** 221, 222. 1940. [*B. longirostris.*]

Weissenböck, G. Über der Flavonoidstoffwechsel während der Samenkeimung. (English summary.) Ber. Deutsch. Bot. Ges. **83:** 79–83. 1970. [*B. vulgaris*; quercetin and kaempferol glycosides.]

Wiinstedt, K. Vore *Barbarea*-Arter. Bot. Tidsskr. **41:** 434–436. 1931. [Interspecific hybridization between *B. vulgaris* (including *B. arcuata*) and *B. intermedia*; key to species.]

Zennie, T. M., & C. D. Ogzewalla. Ascorbic acid and vitamin A content of edible and wild plants of Ohio and Kentucky. Econ. Bot. **31:** 76–79. 1977. [*B. vulgaris.*]

29. **Iodanthus** Torrey & A. Gray ex Steudel, Nom. Bot. ed. 2. **1**: 812. 1840.[8]

Perennial herbs [or subshrubs]. Stems usually single at base, often branched above, glabrous or sparsely [to densely] pubescent with unbranched trichomes. Leaves petiolate, lanceolate to ovate [or cordate], amplexicaul to auriculate [or not auriculate], glabrous to glabrescent [or hirsute with unbranched or bifurcate trichomes]; lower leaves usually lyrate, with 1–9 pairs of lateral lobes [or undivided]; petioles winged [or wingless]. Inflorescence an ebracteate, elongate [or corymbose] raceme; fruiting pedicels ascending to divaricate, smooth [or striate]. Sepals erect, oblong, glabrous or with a subapical tuft of trichomes [or hirsute on the outside], usually membranaceous at margin. Petals white, lavender, purple, violet [or yellow], spatulate to obovate, much longer than [or about as long as] the sepals. Stamens 6, tetradynamous [or nearly equal in length], slightly exserted [or included]. Nectar glands forming a well-developed ring subtending the bases of median [or all] filaments and surrounding those of lateral ones. Fruits linear, terete [or slightly compressed parallel to the septum], sessile or borne on gynophores less than 1 mm long, glabrous [or sparsely hirsute]; valves conspicuously 1-nerved; styles thick, long [or obsolete]; stigmas entire, capitate. Seeds uniseriately arranged in each locule, wingless, reticulate, oblong; cotyledons accumbent to incumbent. (Including *Chaunanthus* O. E. Schulz, *Oclorosis* Raf.) TYPE SPECIES: *I. pinnatifidus* (Michx.) Steudel. (Name from Greek *iodes,* violet, and *anthos,* flower.)—PURPLE ROCKET, VIOLET ROCKET.

A New World genus of four species, three of which are narrowly endemic to Mexico. Each of the Mexican species has been collected just a few times and from only one area. The fourth is widely distributed in the United States, particularly in the Midwestern States (Ohio, Indiana, Illinois, and Missouri). *Iodanthus pinnatifidus* (Michx.) Steudel (*Hesperis pinnatifida* Michx., *Thelypodium pinnatifidum* (Michx.) S. Watson, *Cheiranthus hesperidoides* Torrey & A. Gray, *I. hesperidoides* (Torrey & A. Gray) A. Gray), purple rocket, violet rocket, occupies an area immediately west of the Appalachian Mountains and east of the 100th meridian. It grows primarily on alluvial soil in moist,wooded ravines and floodplain woods, as well as along stream banks, in southwestern Pennsylvania and adjacent northwestern West Virginia south into Tennessee (Cannon, Cheatham, Davidson, Houston, Knox, Rutherford, Stewart, and Williamson counties) and northwestern Alabama (Colbert, Lauderdale, and Lawrence counties), west into Arkansas (Baxter, Benton, Hempstead, Lawrence, Madison, Marion, and Newton counties) and eastern and central Texas, and north into northeastern Oklahoma, eastern Kansas, central Iowa, and southeastern Minnesota. It was reported by Small (1903, 1933) and Britton & Brown from Louisiana, but I have not seen any specimens from there, and MacRoberts did not include it in his checklist.

Iodanthus pinnatifidus is distinguished from the Mexican species of the genus

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[8] Most floras wrongly cite Torrey & Gray (Fl. N. Am. 1: 72. 1838) as the authors of the genus. As shown by Rollins, however, these authors neither recognized *Iodanthus* as a genus nor assigned a legitimate specific name to it. Steudel should be credited for validating the generic name.

by its herbaceous habit, glabrescent, usually auriculate leaves, petioles with winged margins, and petals usually twice as long as the sepals. *Iodanthus petiolatus* (Hemsley) Rollins (Hidalgo), *I. acuminatus* Rollins (Jalisco), and *I. mexicanus* Rollins (Puebla) are shrubby and have pubescent leaves without auricles, wingless petioles, and petals slightly longer than the sepals.

There is little agreement on the tribal disposition of *Iodanthus*. Von Hayek and Moggi closely associated it with *Hesperis* L. and *Erysimum* (as *Cheiranthus* L.) of the tribe Hesperideae, while Schulz placed one of its species in the Matthioleae and another (as *Chaunanthus*) in the Sisymbrieae DC. The association of *Iodanthus* by these authors with some of the Old World genera was not well founded. On the basis of the cellular pattern of the septum, Dvořák suggested that *Iodanthus* be excluded from the Hesperideae and associated with the Cardamininae as circumscribed by Prantl. Robinson's close association of *Iodanthus* with *Barbarea* in the tribe Arabideae is the most acceptable placement. *Iodanthus* is distinguished from *Barbarea* in having purple or white flowers, undivided, petiolate upper cauline leaves, and nontorulose fruits. The Mexican species of *Iodanthus* have yellow flowers, but they are all subshrubs with undivided, pubescent leaves.

Nothing is known about the floral biology, cytology, embryology, anatomy, chemistry, genetics, or ecology of *Iodanthus*. The genus has no economic value.

REFERENCES:

Under family references in AL-SHEHBAZ (Jour. Arnold Arb. **65:** 343–373. 1984), see BRITTON & BROWN; FERNALD; VON HAYEK; MURLEY; RICKETT; SCHULZ; SMALL; and E. B. SMITH.

Under tribal references see CORBETT; CORRELL & CORRELL; ELLIS *et al.*; GATTINGER; GODFREY & WOOTEN; HEBEL; MACROBERTS; MCKINNEY; MOHR; ROLLINS *et al.*; SHARP *et al.*; and SMALL.

DVOŘÁK, F. Does the genus *Iodanthus* Torr. & Gr. subsume under the tribe Hesperideae? Phyton Austria **14:** 113–117. 1970. [No.]

EASTERLY, N. W. Distribution patterns of Ohio Cruciferae. Castanea **29:** 164–173. 1964. [*I. pinnatifidus,* 168, *map.*]

MOGGI, G. Osservazioni tassonomiche e corologiche sulle Hesperideae (Cruciferae). Webbia **20:** 241–273. 1965.

MOHLENBROCK, R. H. The illustrated flora of Illinois. Flowering plants: willows to mustards. xii + 286 pp. London and Amsterdam. 1980. [*I. pinnatifidus,* 114–116, *fig. 48, map.*]

MORLEY, T. Spring flora of Minnesota. 283 pp. Minneapolis. 1966. [*I. pinnatifidus,* 139, 140.]

PRANTL, K. Cruciferae. *In:* A. ENGLER & K. PRANTL, eds., Nat. Pflanzenfam. III. **2:** 145–206. 1891. [*Iodanthus,* 183.]

ROBINSON, B. L. *Iodanthus. In:* A. GRAY & S. WATSON, Synopt. Fl. N. Am. **1:** 104, 150. 1895.

ROLLINS, R. C. A systematic study of *Iodanthus.* Contr. Dudley Herb. **3:** 209–215. 1942. [Treatment of four species.]

STEYERMARK, J. A. Flora of Missouri. lxxxiii + 1725 pp. Ames, Iowa. [1963.] [*I. pinnatifidus,* 761, *map.*]

STRAUSBAUGH, P. D., & E. L. CORE. Flora of West Virginia. ed. 2. xl + 1079 pp. Grantsville. [1978.] [*I. pinnatifidus,* 434.]

30. **Leavenworthia** Torrey, Ann. Lyc. Nat. Hist. New York **4:** 87. 1837.

Herbaceous, glabrous, taprooted, winter annuals. Leaves petiolate, the earlier ones entire, the later ones progressively more pinnately divided, the mature leaves lyrately pinnatifid, usually forming well-developed rosettes; lateral lobes absent or 1–10, entire to coarsely dentate; terminal lobe entire to prominently angled, markedly or only slightly larger than the adjacent pair of lateral lobes. Early flowers always solitary, borne on scapes 3–15 cm long that originate from center of the rosette; later flowers long pedicellate, borne in lax, ebracteate, few- to many-flowered racemes that arise from the axils of rosette leaves. Sepals narrowly oblong to linear, spreading to erect, glabrous, equal, not saccate or only slightly so at base. Petals much longer than sepals, obovate to oblanceolate, clawed; blades white to lavender or yellow, horizontal to ascending, shallowly to deeply emarginate or sometimes truncate to obtuse; claws erect, much shorter than blades, yellow to orange distally. Nectar glands 4, lobed, the median pair subtending bases of the paired stamens, the lateral pair surrounding those of the single stamens. Stamens 6, strongly tetradynamous; filaments white, erect, linear, unappendaged; anthers oblong, introrse or those of paired stamens sometimes extrorse. Fruits linear to oblong or subglobose, terete or strongly flattened parallel to the septum, torulose or smooth, subsessile to short stipitate; valves glabrous, obscurely veined, thin or thick and somewhat fleshy before drying; replum straight to strongly constricted between seeds; septum membranaceous, usually with an obscure midvein; funicles free from septum; styles slender to stout, persistent; stigmas entire to slightly 2-lobed. Seeds orbicular to slightly longer than broad, flattened, uniseriately arranged, winged to marginate, dark brown, nonmucilaginous when wet, prominently reticulate, the areolae of reticulum nearly uniform in size throughout or those of the embryo region smaller than the rest; radicle much shorter than cotyledons, straight or slightly bent and only obscurely accumbent. LECTOTYPE SPECIES: *L. aurea* Torrey; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 189. 1913. (Name commemorating Melines Conkling Leavenworth, Jan. 15, 1796–Nov. 16, 1862, American physician and amateur botanist who collected plants in Florida, Alabama, Louisiana, Arkansas, and Oklahoma.)

A well-defined genus of eight species confined to limestone glades and distributed primarily in the Southeastern States (Tennessee, Georgia, Alabama, Arkansas). Two of the three species that grow outside this area, *Leavenworthia aurea* (Choctaw and McCurtain counties, Oklahoma) and *L. texana* Mahler (St. Augustine County, Texas), are narrow endemics, while the third, *L. uniflora* (Michx.) Britton, is the most widely distributed member of the genus (see below). In general, the area occupied by *Leavenworthia* can be divided into an eastern and a western part separated by the Mississippi Alluvial Plain, which has no limestone glades. This accounts for the total absence of the genus in southern Illinois, western Tennessee, Mississippi, Louisiana, and all except the northern portion of Arkansas. The eastern part of the range contains all 12 taxa of the genus except *L. aurea* and *L. texana*; *L. uniflora* occurs in both areas.

Leavenworthia uniflora (Michx.) Britton (*Cardamine uniflora* Michx., *L.*

Michauxii Torrey), $2n = 30$, is the most distinctive and the most widely distributed species of the genus. It occurs from southern Ohio and southern Indiana (Clark County) southward into central and southern Kentucky (12 counties), Tennessee (Bedford, Bledsoe, Hamilton, Knox, Marshall, Maury, Rutherford, and Wilson counties), Georgia (Walker County), and Alabama (Jackson, Lawrence, Madison, Marshall, and Morgan counties). It is disjunct and widely distributed in the Ozark region of Arkansas (Baxter, Benton, Carroll, Marion, Randolph, and Sharp counties) and in central and southern Missouri (33 counties). The wide geographic distribution of *L. uniflora* can be attributed to autogamy, weedy tendencies, high seed production, and adaptation to habitats drier than those occupied by the other taxa of the genus (Rollins, 1963, 1981). *Leavenworthia uniflora* is easily distinguished by its highly dissected leaves with coarsely dentate lobes, the terminal one of which is only slightly larger than the adjacent lateral ones, its truncate or rounded petals to 7 mm long, and its subaccumbent radicle.

A close relative and morphologically very distinct, *Leavenworthia torulosa* A. Gray ($2n = 30$) is widespread on limestone barrens of central Tennessee (Bedford, Bradley, Davidson, Giles, Lincoln, Marshall, Maury, Rutherford, Sumner, Williamson, and Wilson counties). It is endangered in Kentucky, where it is known only from a few glades in Logan, Simpson, and Warren counties. Several authors (e.g., Baskin & Baskin, 1984; Freeman *et al.*; Mohr; Small, 1933) have recorded *L. torulosa* from Alabama, but all their reports are apparently based on Mohr's collection from Madison County, which is probably the only known record of the species from that state.

Kotov's report of *Leavenworthia torulosa* from the banks of the Oskol River (Belgord Province, central Russia) and from a swamp near Kuya (Archangel Province, northern Russia) was based on collections made in 1915 and 1912, respectively. Kotov did not discuss the origin of these two collections, but it is highly unlikely that they were made from natural populations in Russia. The species is not weedy nor does it grow outside its native range.

The fruits of *Leavenworthia torulosa* are conspicuously torulose even when young, the seeds are wingless to obscurely winged, and the areolae of the seed coat are nearly uniform throughout. These features should distinguish the species easily from the other leavenworthias.

Leavenworthia stylosa A. Gray ($2n = 30$) is endemic to central Tennessee (Bedford, Davidson, Rutherford, Smith, and Wilson counties). It was said to grow in Williamson County (Sharp *et al.*), but neither Rollins (1963) nor Kral has indicated that it grows there, and I have not seen any material from that county. It is likely that the record was based on misidentified plants of *L. torulosa*. *Leavenworthia stylosa* has the largest flowers and longest styles in the genus and is self-incompatible. In some populations flower color is uniformly yellow, while in others it ranges from white to various shades of lavender. Rollins (1963) observed a gradual mixing of the two major color forms in populations west of Gladeville, Tennessee. In the related *L. torulosa* and *L. uniflora* (both self-compatible) the flowers are smaller and white to lavender. The fruits of *L. stylosa* show a wide range of variation in shape and length. In one collection, *Rollins 59104* (GH!), they are oblong to ovate and only about

0.5 cm long, while in another, *Rollins 53143* (GH!), they are linear and to 4.5 cm long. The variation in fruit morphology, however, is continuous and does not support the division of the species into infraspecific taxa.

Both varieties of *Leavenworthia crassa* Rollins ($2n = 22$) are narrowly endemic to northern Alabama. Varietas *crassa* grows in Lawrence, Marshall, and Morgan counties, while var. *elongata* Rollins is restricted to the last two counties. The fruits in var. *crassa* are 6–10 mm long, the styles are 3–6 mm long, and the petals are 10–13 mm long and white to yellow. Varietas *elongata* has slightly longer (8–12 mm) fruits, shorter (2.5–3.5 mm) styles, and shorter (9–11 mm), yellow petals. Kral (p. 494) has mapped var. *crassa* as occurring in Davidson County, Tennessee. It is possible that this disjunct record is based on plants of *L. stylosa* with very short fruits. The fruits in both *L. stylosa* and *L. crassa* are fleshy when green and have thick valves when dry, but they overlap only slightly in their length, which is rarely less than 1 cm in the former and rarely more than that in the latter. However, the two species differ in chromosome number and in their radicle, which is straight in *L. crassa* and curved in *L. stylosa.*

Another narrow endemic of northern Alabama is *Leavenworthia alabamica* Rollins, $2n = 22$. Rollins (1963) recognized two varieties: var. *alabamica* (Colbert, Franklin, Lawrence, and Morgan counties) and var. *brachystyla* Rollins (Marshall and Morgan counties). The former has styles 2.5–5.5 mm long and fruits acute at apex and base, while the latter has styles 1.5–3 mm long and fruits rounded at both ends. The species is most closely related to *L. crassa* and *L. exigua* Rollins ($2n = 22$). It differs from *L. crassa* in having fruits that are flattened, nonfleshy, and 1.5–3 cm long, with more than 12 nonoverlapping seeds, instead of terete, fleshy, and 0.6–1.2 mm long, with no more than ten overlapping seeds. *Leavenworthia alabamica* is distinguished from *L. exigua* in having deeply emarginate petals 10–14 mm long, slightly longer (1.5–5.5 mm) styles, and fruits 3–4.5 mm wide with more than 12 seeds. In *L. exigua* the petals are shallowly emarginate and 6–9 mm long, the styles are 1–3 mm long, and the fruits are 3.5–5.5 mm wide with only 4–10 seeds.

Leavenworthia exigua consists of three varieties, one of which, var. *laciniata* Rollins, is endemic to northern Kentucky (Bullitt and Jefferson counties). Varietas *exigua* is distributed in Georgia (Catoosa and Walker counties) and Tennessee (Bedford, Davidson, Decatur, Hardin, Marshall, Maury, Rutherford, Williamson, and Wilson counties), whereas var. *lutea* Rollins is endemic to Alabama (Jefferson, Marshall, and St. Clair counties) and Tennessee (Maury County). The flowers are yellow in var. *lutea* and white to light lavender in the other two. Varietas *exigua* has lavender sepals and styles 1–2 mm long, while var. *laciniata* has green sepals and styles 2–3 mm long.

Most records of *Leavenworthia aurea* from Tennessee, Georgia, and Alabama belong to *L. exigua* (Rollins, 1956). The former is so strikingly similar to *L. exigua* var. *lutea* (both with yellow flowers) that the casual observer cannot tell them apart. However, *L. aurea* is a polyploid ($2n = 48$) restricted to portions of southeastern Oklahoma. It is distinguished from *L. exigua* by having thick- (vs. thin-)margined fruits and rounded (vs. angular) terminal leaf lobes. Varietas *lutea* also resembles *L. texana* ($2n = 22$) in flower color, leaf-lobe shape,

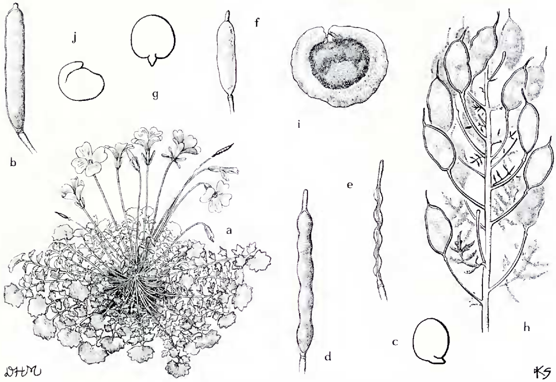

FIGURE 3. **Leavenworthia** and **Selenia.** a, *Leavenworthia stylosa,* plant with flowers, × ½—note single-flowered scapes from center of basal rosette. b, c, *L. uniflora:* b, fruit, × 1; c, embryo, × 10. d, e, *L. torulosa:* d, fruit, valvular view, × 1; e, fruit, lateral view, × 1. f, *L. exigua,* fruit, × 1. g, *L. alabamica,* embryo, × 10—note straight radicle. h–j, *Selenia aurea:* h, infructescence, × 1—note bracts; i, seed, × 6; j, embryo, × 6.

and chromosome number. However, it differs in having shorter styles (1–2 vs. 2–3.5 mm) and thin- (vs. thick-)margined fruits.

Although *Leavenworthia* has no known immediate generic relative, it is probably more closely related to *Selenia* than to any other genus of the Cruciferae (Torrey). Both genera are glabrous annuals with dissected leaves, often yellow flowers, spreading sepals, short gynophores, flattened fruits, somewhat thick valves, winged seeds, and prominently reticulate, thick seed coats. *Leavenworthia* is easily distinguished by its inflorescences and seeds. The early flowers are in solitary scapes that arise from the center of a rosette (FIGURE 3a), while the later ones are in ebracteate racemes. The seeds have straight or slightly curved radicles that are much shorter than the cotyledons (FIGURE 3c, g). *Selenia* has bracteate inflorescences and accumbent cotyledons.

Von Hayek derived *Leavenworthia* directly from *Cardamine* and considered the genus to be ancestral to the monotypic North American *Idahoa* A. Nelson & Macbr. (as *Platyspermum* W. J. Hooker) and the Caucasian *Pseudovesicaria* (Boiss.) Rupr. Schulz also suggested a close association with *Cardamine* and placed *Leavenworthia* between the Asiatic *Loxostemon* and *Pegaeophyton.* In my opinion, *Leavenworthia* is not related to any of these genera, and I agree with Rollins (1963) that it should not be associated with *Cardamine.*

All species of *Leavenworthia* are winter annuals very closely adapted to glades that are usually associated with red cedar, *Juniperus virginiana* L. They grow primarily on a thin layer of soil overlying flat-bedded outcrops of dolomitic limestone. The glades are often waterlogged from late autumn to early spring, but they become very dry during the summer. As stated by Rollins (1963, p. 6), "this close adaptation to a rather narrow and rigid set of edaphic conditions appears to have been an important factor influencing the direction and extent of evolution within the genus." Seeds of all species of *Leavenworthia* remain dormant during the summer (Baskin & Baskin, 1971). Germination takes place in early fall, and the plants persist through winter as slow-growing rosettes. Blooming may start as early as late February and often continues through April, while seed maturity is usually reached by mid or late May. All species are capable of growing in soils fully saturated with water, and their roots are metabolically adapted to grow under anaerobic conditions (Baskin & Baskin, 1976).

All species except for the widespread *Leavenworthia uniflora* are listed as endangered or threatened (Kral). Man's conversion of the limestone barrens in the Southeast to pastures or industrial and housing developments has altered or destroyed the habitats of *Leavenworthia.* Although a few species are successful in moving onto cornfields, wastelands, and pastures, it is highly unlikely that they will persist in such unstable habitats. During favorable seasons, plants of all species may produce numerous rosette leaves, scapes, and racemes, but under poor edaphic conditions they may produce one to only a few leaves and single-flowered scapes. This aspect of variation in *Leavenworthia* has been well documented by Rollins (1963, *pls. 7–15*).

The reproductive biology of *Leavenworthia* has been thoroughly studied, particularly in relation to breeding systems, population variability, petal-color polymorphism, insect pollination, genetics of self-incompatibility, racial differentiation, interspecific hybridization, and evolution of self-compatibility and autogamy (see Lloyd, Rollins, and Solbrig and references therein). Self-incompatibility was found in all populations of *L. stylosa* tested, but in only one of four races of *L. alabamica* and four of 15 of *L. crassa* (Lloyd, 1965). The remaining species are self-compatible, and only *L. uniflora* is highly autogamous. According to Lloyd (1968a), there is no absolute distinction between self-compatibility and self-incompatibility in either *L. alabamica* or *L. crassa,* and partial unilateral incompatibility has involved quantitative, rather than qualitative, changes in pollen-stigma relationships, which have been gradual, with allele changes at many loci.

Self-compatibility in *Leavenworthia* has arisen independently at least three (Rollins, 1963) or six (Lloyd, 1969) times. The shift from self-incompatibility to self-compatibility is a major trend in the genus and has accompanied the evolution of well-marked varieties in both *L. alabamica* and *L. crassa* (Rollins, 1963). More than 15 evolutionary trends have accompanied this shift in the reproductive system (Lloyd, 1969). The most obvious ones are decrease in length of sepals, petals, anthers, and styles, reduction of petal emargination, and increase in ovule number. Some other changes are from extrorse to introrse anthers of median stamens, from flaring to erect petals, and from odoriferous to nonodoriferous flowers.

All species of *Leavenworthia* are very closely adapted to specific edaphic conditions (see above), and they usually flower at periods when the pollinating insects are very scarce. The lack of sufficient pollinators and the need for adequate seed set may have been the most important selective forces that favored the shift from self-incompatibility to self-compatibility. The autogamous *L. uniflora* and *L. exigua* var. *exigua* are more widespread than the self-incompatible taxa, and both usually flower a few weeks earlier.

When species of *Leavenworthia* are sympatric, the self-incompatible ones occupy wetter parts of the glade than the self-compatible ones. The self-incompatible taxa can therefore grow for longer periods and can be pollinated before the advent of drought. In the drier glades these plants are under water stress when the pollinators emerge and are therefore unable to produce sufficient seeds to compete with the self-compatible taxa in the next generations (Solbrig & Rollins).

Lloyd (1965, 1969) observed that honey bees, *Apis mellifera* L. (Apidae), were the most frequent visitors to the flowers of *Leavenworthia crassa* and *L. stylosa*; they comprised 57–70 percent of the total insect visitors. Twenty species of solitary bees, particularly of the genera *Andrena* (Andrenidae), *Halictus* and *Dialictus* (Halictidae), and *Ceratina* (Apidae), made up about 15 percent. The remaining insects were flies, butterflies, and beetles. With the exception of *Bombylius major* L. (Bombyliidae), visiting insects did not discriminate among the flower-color morphs. Individuals of this species, however, showed a significant preference for yellow-centered flowers and rarely visited other flower morphs.

Variation in flower color has been thoroughly studied by Rollins (1963) and Lloyd (1969). The number of flower-color morphs is higher in self-incompatible than in self-compatible taxa. Lloyd has suggested that in *Leavenworthia crassa* the difference between the yellow and the yellow-centered flowers is determined by a single locus and that in one race yellow is dominant while in three others it is recessive. In crosses between races, the incomplete dominance of the yellow-centered and yellow forms indicates that the dominant relationships in each population depend on polygenic modifiers.

On the bases of morphology, chromosome numbers, and breeding systems, two major lines of evolution are recognized in *Leavenworthia.* Three species, *L. stylosa, L. torulosa,* and *L. uniflora,* have a diploid number of 30 and have embryos with curved radicles and subaccumbent cotyledons (FIGURE 3c). The first species is self-incompatible and is the most primitive in the group, whereas the last is autogamous and the most advanced. In the second line, four species (*L. alabamica, L. crassa, L. exigua, L. texana*) have $2n = 22$ and embryos with straight radicles (FIGURE 3g). *Leavenworthia aurea* ($2n = 48$), which also has straight radicles, ties in very well with *L. exigua* var. *lutea* and *L. texana.* Embryos with straight radicles are not known elsewhere in the Cruciferae. It is likely, therefore, that the two groups of species have evolved from ancestors with curved radicles. Baldwin stated that species with $2n = 30$ are hexaploid and that *L. exigua* (as *L. aurea*) is an aneuploid derived from ancestral tetraploids with $2n = 20$. These assumptions, however, are unsupported, and all species except *L. aurea* are diploid (Rollins, 1963).

In numerous cedar glades of the Central Basin of Tennessee (Bedford, Davidson, Marshall, Maury, Rutherford, and Wilson counties), various combinations of four species (*Leavenworthia exigua, L. stylosa, L. torulosa,* and *L. uniflora*) grow sympatrically within inches of one another. All are reproductively isolated in nature, and either they cannot be crossed experimentally, or (as in the combination *L. stylosa* × *L. exigua*) their first-generation hybrid is completely sterile. The remaining species of the genus are largely allopatric. Although both *L. alabamica* and *L. crassa* grow in the same general area in northern Alabama, their ranges rarely overlap. However, in Morgan County *L. alabamica* var. *brachystyla* hybridizes with both varieties of *L. crassa,* and their natural interspecific hybrids, which often grow in pastures and cultivated fields, are fully fertile. Meiosis is normal in the artificial hybrids of both species, and only occasional irregularities have been observed (Rollins, 1963).

The chemistry of *Leavenworthia* has not been studied adequately, and only in *L. torulosa* have the seeds been analyzed for fatty acids (Miller *et al.*). The species has a high concentration (53 percent) of eicosenoic acid and lacks erucic acid. In this, *Leavenworthia* resembles the closely related *Selenia* (see below). The same fatty-acid pattern, however, also occurs in the unrelated *Lobularia* Desv. and *Teesdalia* R. Br., of the tribes Alysseae and Lepidieae, respectively.

The seeds of *Leavenworthia* are probably dispersed over short distances by rain-washes, and for longer ones by water in areas where populations grow adjacent to streams. Lloyd (1965) suggested that the seeds lack adaptations for either animal or wind dispersal and that their poor dispersal may have effectively isolated various populations.

The genus has no economic value. The flowers of both *Leavenworthia stylosa* and *L. crassa* are very showy, and both species might well be used as ornamentals.

REFERENCES:

Under family references in AL-SHEHBAZ (Jour. Arnold Arb. **65:** 343–373. 1984), see BRITTON & BROWN; EASTERLY (1964); FERNALD; VON HAYEK; MURLEY; RICKETT; ROLLINS (1966, 1981); ROLLINS & RÜDENBERG (1977); SCHULZ; SMALL; and E. B. SMITH.

Under tribal references see CORRELL & CORRELL; DUNCAN & KARTESZ; FREEMAN *et al.*; GATTINGER; HEBEL; MILLER *et al.*; MOHR; ROLLINS *et al.*; SHARP *et al.*; and SMALL.

AYENSU, E. S., & R. A. DEFILIPPS. Endangered and threatened plants of the United States. xv + 403 pp. Washington, D. C. 1978. [*Leavenworthia,* six taxa of four species are endangered, 76.]

BALDWIN, J. T., JR. Chromosomes of Cruciferae—II. Cytogeography of *Leavenworthia.* Bull. Torrey Bot. Club **72:** 367–378. 1945. [*L. exigua* (as *L. aurea*), *L. stylosa, L. torulosa, L. uniflora*; chromosome numbers, distributions, breeding systems.]

BANGMA, G. S. Temperature and related factors affecting germination and flowering of *Leavenworthia stylosa* (Cruciferae). 52 pp. Unpubl. M.A. thesis, Vanderbilt Univ., Nashville, Tennessee. 1966.*

BASKIN, J. M., & C. C. BASKIN. Germination regulating mechanisms in *Leavenworthia* spp. (Cruciferae). (Abstr.) ASB Bull. **17:** 30. 1970. [Seed dormancy of *L. stylosa, L. torulosa,* and *L. uniflora.*]

——— & ———. Germination ecology and adaptation to habitat in *Leavenworthia* spp. (Cruciferae). Am. Midl. Nat. **85:** 22–35. 1971. [*L. stylosa, L. torulosa, L. uniflora*;

germination is prevented in late spring and early summer by internal dormancy mechanisms that are overcome by a short period of after-ripening.]

——— & ———. The ecological life cycle of the cedar glade endemic *Leavenworthia exigua* var. *exigua*. Canad. Jour. Bot. **50:** 1711–1723. 1972a. [Habitats, plant associations, germination, phenology, effects of temperature, flowering.]

——— & ———. Influence of germination date on survival and seed production in a natural population of *Leavenworthia stylosa*. Am. Midl. Nat. **88:** 318–323. 1972b.

——— & ———. A contribution to the ecological life cycle of *Leavenworthia stylosa*. Jour. Tenn. Acad. Sci. **47:** 91–93. 1972c.

——— & ———. *Leavenworthia exigua* var. *lutea* in Tennessee cedar glades. Castanea **38:** 195, 196. 1973. [First report for Tennessee from Maury County.]

——— & ———. Evidence for metabolic adaptation to flooding in *Leavenworthia uniflora*. Jour. Chem. Ecol. **2:** 441–447. 1976. [Adaptation to water-logged soil was determined by measuring the activity of alcohol dehydrogenase.]

——— & ———. *Leavenworthia torulosa* Gray: an endangered plant species in Kentucky. Castanea **42:** 15–17. 1977. [Known from a few small populations in Warren and Logan counties.]

——— & ———. The rarity of *Leavenworthia uniflora*, with special reference to its occurrence in Kentucky. *Ibid.* **43:** 54–57. 1978a.

——— & ———. The seed bank in a population of an endemic plant species and its ecological significance. Biol. Conserv. **14:** 125–130. 1978b. [*L. stylosa*.]

——— & ———. Geographical distribution and notes on the ecology of the rare endemic *Leavenworthia exigua* var. *laciniata*. Castanea **46:** 243–247. 1981. [Distribution in Bullitt and Jefferson counties, Kentucky.]

——— & ———. On the historical occurrence of two cedar glade endemics in Alabama, and a discussion of Mohr's yellow-flowered *Leavenworthia*. *Ibid.* **49:** 167–171. 1984. [*L. exigua, L. torulosa, L. uniflora*.]

——— & ———. Distribution and geographical/evolutionary relationships of cedar glade endemics in southeastern United States. ASB Bull. **33:** 138–154. 1986. [County distributions of ten taxa of *Leavenworthia*.]

Caudle, C., & J. M. Baskin. The germination pattern of three winter annuals. Bull. Torrey Bot. Club **95:** 331–335. 1968. [*L. crassa*.]

Cranfill, R., J. M. Baskin, & M. E. Medley. Taxonomy, distribution and rarity status of *Leavenworthia* and *Lesquerella* (Brassicaceae) in Kentucky. Sida **11:** 189–199. 1985. [*L. exigua* var. *laciniata, L. torulosa, L. uniflora*; key, distributions, map.]

Gray, A. The genus *Leavenworthia*. Bot. Gaz. **5:** 25–27. 1880. [*L. aurea, L. stylosa, L. torulosa, L. uniflora* (as *L. Michauxii*).]

Hooker, J. D. *Leavenworthia aurea*. Bot. Mag. **94:** *pl. 5730*. 1868. [Illustrations and description are of *L. stylosa*, rather than *L. aurea*.]

Kotov, M. I. New American genus and species *Leavenworthia torulosa* A. Gray (Brassicaceae) in the USSR. (In Russian.) Bot. Zhur. **60:** 1187, 1188. 1975.

Kral, R. A report on some rare, threatened, or endangered forest-related plants of the South. U. S. Dep. Agr. Forest Serv. South. Reg. Tech. Publ. R8-TP2. Vol. 1. x + 718 pp. 1983. [*Leavenworthia*, 480–507; descriptions, habitats, maps.]

Lloyd, D. G. Breeding systems and evolution in *Leavenworthia* (Cruciferae). 318 pp. Unpubl. Ph.D. dissertation, Harvard Univ., Cambridge, Massachusetts. 1964.

———. Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). Contr. Gray Herb. **195:** 1–134. 1965. [*L. alabamica, L. crassa*; 19 races recognized; breeding systems, hybridization, dispersal, pollination.]

———. The genetics of self-incompatibility in *Leavenworthia crassa* Rollins (Cruciferae). Genetica **38:** 227–242. 1967. [One-locus sporophytic self-incompatibility.]

———. Pollen tube growth and seed set in self-incompatible and self-compatible *Leavenworthia* (Cruciferae) populations. New Phytol. **67:** 179–195. 1968a. [*L. alabamica, L. crassa*.]

———. Partial unilateral incompatibility in *Leavenworthia* (Cruciferae). Evolution **22:** 382–393. 1968b. [Crosses between nine self-compatible and self-incompatible races of *L. alabamica* and *L. crassa.*]

———. Petal color polymorphism in *Leavenworthia* (Cruciferae). Contr. Gray Herb. **198:** 9–40. 1969. [Twenty-nine geographic races, seven species; variation in petal color, genetic basis of color inheritance, insect pollination.]

LYONS, E. E. The evolutionary significance of breeding system variation in *Leavenworthia crassa* Rollins (Cruciferae). 186 pp. Unpubl. Ph.D. dissertation, Duke Univ., Durham, North Carolina. 1986.* [See Diss. Abstr. Int. **47:** 4747B, 4748B. 1987.]

MAHLER, W. F. Notes on rare Texas and Oklahoma plants. Sida **9:** 76–86. 1981. [*L. aurea,* 83, *fig. 6.*]

———. *Leavenworthia texana* (Brassicaceae), a new species from Texas. Sida **12:** 239–242. 1987. [Relationship to *L. aurea,* key, chromosome numbers.]

ROLLINS, R. C. Some Cruciferae of the Nashville Basin, Tennessee. Rhodora **54:** 182–192. 1952. [*Leavenworthia,* 182.]

———. The problem of *Leavenworthia aurea. Ibid.* **58:** 73–76. *pl. 1223.* 1956. [*L. exigua,* sp. nov.]

———. The evolution and systematics of *Leavenworthia* (Cruciferae). Contr. Gray Herb. **192:** 3–98. 1963. [The basic treatment; detailed accounts of cytology, interspecific hybridization, breeding systems, growth cycle, distributions, evolutionary trends, and taxonomy.]

SOLBRIG, O. T. Breeding system and genetic variability as revealed by isozymes in the genus *Leavenworthia.* (Abstr.) Am. Jour. Bot. **57:** 764. 1970.

———. Genetic variation in populations of *Leavenworthia* (Cruciferae). (Abstr.) *Ibid.* **58:** 466. 1971.

———. Breeding system and genetic variation in *Leavenworthia* (Cruciferae). Evolution **26:** 155–160. 1972. [Patterns of variation in six isozyme systems in 11 populations of six species.]

———. On the relative advantages of cross- and self-fertilization. Ann. Missouri Bot. Gard. **63:** 263–276. 1976. [*Leavenworthia,* 273–275.]

——— & R. C. ROLLINS. The evolution of autogamy in species of the mustard genus *Leavenworthia.* Evolution **31:** 265–281. 1977. [*L. alabamica, L. crassa, L. exigua, L. stylosa.*]

TAYLOR, R. J., & C. S. TAYLOR. An annotated list of rare or infrequently collected vascular plants that grow in Oklahoma. Publ. Herb. Southeastern Okla. State Univ. Durant **2:** 15–120. 1978. [*L. aurea,* 55, 56, 85.]

THOMAS, J. L. Plants. Pp. 5–12 *in* H. BOSCHUNG, ed., Endangered and threatened plants and animals of Alabama. Bull. Alabama Mus. Nat. Hist. Vol. 2. 1976. [*L. alabamica* var. *brachystyla, L. crassa* vars. *crassa* and *elongata,* and *L. exigua* var. *lutea* are endangered; *L. alabamica* and *L. torulosa* are threatened; 6, 8.]

TORREY, J. An account of several new genera and species of North American plants. Ann. Lyc. Nat. Hist. New York **4:** 80–94. *pls. 4, 5.* 1837. [*Leavenworthia,* 87–94.]

WAITS, E. D. Autecological studies of *Leavenworthia stylosa,* a cedar glade endemic. Unpubl. M.A. thesis, Vanderbilt Univ., Nashville, Tennessee. 1964.*

WOLF, F. T. *Peronospora parasitica* on *Leavenworthia.* Jour. Tenn. Acad. Sci. **34:** 3, 4. 1959. [*L. exigua.*]

ZAGER, R. D. Autecological studies on *Leavenworthia stylosa* (Cruciferae). (Abstr.) ASB Bull. **7:** 41. 1960.

———. Studies on seed dormancy and germination in *Leavenworthia stylosa* (Cruciferae). 30 pp. Unpubl. M.A. thesis, Vanderbilt Univ., Nashville, Tennessee. 1962.*

———, E. QUARTERMAN, & E. D. WAITS. Seed dormancy and germination in *Leavenworthia stylosa* (Cruciferae). Jour. Tenn. Acad. Sci. **46:** 98–102. 1971. [Germination depends on the combined effects of alternate wetting and drying, lapse of time, and moderate temperature during autumn.]

31. **Selenia** Nuttall, Jour. Acad. Nat. Sci. Phila. **5:** 132. 1825.

Glabrous, caulescent [or acaulescent with crown usually swollen], spring-flowering annuals. Leaves subsessile [or short to long petiolate], pinnately [or bipinnately] dissected, with numerous entire to dentate or divided lobes, the rachis marginate or winged. Inflorescences bracteate terminal racemes, usually elongated in fruit [or flowers solitary on scapes arising from the axils of rosette leaves in acaulescent taxa]; bracts leafy, pinnately dissected, smaller and less divided upward; rachis of infructescence angled [or terete]; fruiting pedicels slender to stout, spreading to ascending, 1–2.5[–21] cm long. Sepals spreading, slightly unequal and convex at base, caducous [or persistent to fruit maturity], without [or with] a well-developed subapical, hornlike appendage on the exterior, usually membranaceous at margin. Petals yellow, spatulate [to obovate], gradually narrowed to claws, rounded [to emarginate]. Median nectar glands 4 [or 2], lateral gland with [or without] an adaxial lobe and 2 [or 1] abaxial one(s). Stamens 6, tetradynamous; filaments linear, unappendaged; anthers oblong [to ovate or lanceolate], sagittate at base. Fruits dehiscent, narrowly elliptic to broadly oblong [or obovate to globose], compressed parallel to the septum [or inflated], stipitate [or sessile]; valves glabrous [or vesicular], papery [or rather thick], obscurely reticulately veined, the midrib absent; replum flattened to winged [or rounded]; septum complete or incomplete, hyaline, without [or with] a midvein; styles persistent, slender [to stout], strongly flattened [or terete] at base; stigmas capitate, entire [or 2-lobed]. Seeds [3–]6–12[–20], orbicular, flattened, prominently reticulate, broadly winged [or marginate] all around, emarginate at the hilum, biseriately arranged, nonmucilaginous when wet; funicles slender, short, free from septum; cotyledons accumbent, much longer than the radicle. TYPE SPECIES: *S. aurea* Nutt. (Name from Greek *selene,* the moon, in allusion to its superficial resemblance and apparent affinity to *Lunaria.*)

A well-defined genus of four species distributed from central Arkansas and southwestern Missouri west into central New Mexico and south into northeastern Mexico. The genus is represented in the Southeastern States by *Selenia aurea* (*S. aurea* var. *aptera* S. Watson, *S. aptera* (S. Watson) Small), $2n = 46$, which grows on limestone and sandstone barrens and glades, as well as in sandy areas, waste grounds, and cultivated fields. It is widespread in central and western Arkansas (17 counties), southwestern Missouri, southeastern Kansas, and eastern Oklahoma. Although Small and Britton & Brown indicated that it grows in Texas, neither Martin (1940) nor I have seen any specimens from that state. *Selenia aurea* is distinguished from the other selenias by its unappendaged sepals and its pinnate, somewhat reduced leaves that are mostly cauline. In the other species the sepals have a hornlike subapical appendage and the leaves are bipinnate, well developed, and usually basal.

Species of *Selenia* are morphologically very distinct, and they have geographic ranges that rarely overlap. *Selenia dissecta* Torrey & A. Gray (*S. mexicana* Standley), $2n = 14$, is distributed in central New Mexico, the Trans-Pecos region of Texas, and northern Mexico (Coahuila, Nuevo León, and probably Chihuahua). *Selenia Jonesii* Cory occurs mainly in the western part of the Edwards Plateau, Texas, while *S. grandis* R. F. Martin, $2n = 24$, is known only from the lower valley of the Rio Grande, Texas (Cameron, Dimmit, Hidalgo, and La Salle counties). The last species differs from the other selenias in having vesicular fruit valves, persistent sepals, and stout fruiting pedicels to 21 cm long.

The tribal disposition of *Selenia* has not been established adequately. On the basis of its latiseptate, oblong to elliptic fruits, winged seeds, and accumbent cotyledons, several authors (e.g., Bentham & Hooker; Von Hayek; Schulz; Martin, 1940) have closely associated *Selenia* with the Old World genera *Lunaria* L., *Ricotia* L., *Farsetia* Turra, and *Schlechtera* Bolus, all of which are now placed in the tribe Alysseae DC. In my opinion, *Selenia* is not related to any of these genera and should not be placed in the Alysseae. Robinson's inclusion of *Selenia, Leavenworthia,* and *Idahoa* (as *Platyspermum*) in the Arabideae is evidently more appropriate than the association of *Selenia* with any of the Old World genera. These three genera, however, should be associated with each other only loosely. Torrey & Gray proposed the monotypic tribe Selenieae because they believed that the genus is unique in its inverted embryos. Their conclusion, however, was based on erroneous observation. *Selenia* is easily distinguished by its bracteate inflorescences, pinnate or bipinnate leaves, usually appendaged sepals, short-stipitate fruits, and biseriately arranged seeds.

Selenia dissecta and *S. grandis* are both diploid, with $2n = 14$ and 24, respectively, whereas *S. aurea* is a polyploid, with $2n = 46$ (Rollins, 1966; Rollins & Rüdenberg, 1971, 1977). Chromosome numbers should be helpful in tracing evolution within the genus, but more counts are needed, particularly for *S. Jonesii,* which has not been studied cytologically. Rollins and Rüdenberg (1977) observed univalents and multivalents in *S. aurea* and counted $n = 69$ in one and 23 in three greenhouse-grown plants.

Selenia has not been surveyed adequately for secondary constituents, and only *S. grandis* has been analyzed for glucosinolates (Daxenbichler *et al.*) and fatty acids (Mikolajczak *et al.*, 1963). The species is the richest (58 percent) in eicosenoic acid and among the highest (28 percent) in oleic acid of any source within the Cruciferae. It has, however, very low concentrations of linoleic, linolenic, and erucic acids (4, 2, and 3 percent, respectively).

Nothing is known about the reproductive biology, hybridization, anatomy, or ecology of the genus. *Selenia* has no economic importance, and although Nuttall and Hooker recommended *S. aurea* as an ornamental, the genus has not received the horticultural attention it deserves.

REFERENCES:

Under family references in AL-SHEHBAZ (Jour. Arnold Arb. **65:** 343–373. 1984), see BENTHAM & HOOKER; BRITTON & BROWN; FERNALD; VON HAYEK; MURLEY; ROLLINS (1966); ROLLINS & BANERJEE (1979); ROLLINS & RÜDENBERG (1971, 1977); SCHULZ; and E. B. SMITH.

Under tribal references see CORRELL & CORRELL; DAXENBICHLER *et al.*; MIKOLAJCZAK *et al.*; MOORE; ROLLINS *et al.*; and SMALL.

CORY, V. L. A new *Selenia* from the Edwards Plateau of Texas. Rhodora **33:** 142–144. 1931. [*S. Jonesii,* sp. nov.]

DAYTON, W. A. *Selenia dissecta* in New Mexico. Rhodora **41:** 189, 190. 1939.

HOOKER, J. D. *Selenia aurea.* Bot. Mag. **108:** *pl. 6607.* 1882.

HUNTER, C. G. Wildflowers of Arkansas. viii + 296 pp. Little Rock, Arkansas. 1984. [*S. aurea,* 92, 93.]

MAHLER, W. F. Field studies on Texas endemics. Sida **9:** 176–181. 1981. [*S. Jonesii,* 176, *fig. 3.*]

MARTIN, R. F. A new *Selenia* from Texas. Rhodora **40:** 183, 184. 1938. [*S. grandis,* sp. nov.]

———. A review of the cruciferous genus *Selenia.* Am. Midl. Nat. **23:** 455–462. 1940. [Treatment of five species.]

MIKOLAJCZAK, K. L., C. R. SMITH, JR., & I. A. WOLFF. Three new oilseeds rich in cis-11-eicosenoic acid. Jour. Am. Oil Chem. Soc. **40:** 294, 295. 1963. [Seeds of *S. grandis* contain 58 percent eicosenoic acid.]

NUTTALL, T. Description of two new genera of the natural order Cruciferae. Jour. Acad. Nat. Sci. Phila. **5:** 132–135. *pls. 6, 7.* 1825. [*Selenia,* 132–134, *pl. 6.*]

ROBINSON, B. L. Cruciferae. *In:* A. GRAY & S. WATSON, Synopt. Fl. N. Am. **1:** 98–180. 1895. [*Selenia,* 104; generic treatment by S. WATSON, 151.]

STEYERMARK, J. A. Flora of Missouri. lxxxiii + 1725 pp. Ames, Iowa. [1963.] [*Selenia,* 743, map.]

TORREY, J., & A. GRAY. A flora of North America. Vol. 1. xiv + 711 pp. New York. 1838–1840. [*Selenia,* 99, 100.]

32. **Arabis** Linnaeus, Sp. Pl. **2:** 664. 1753; Gen. Pl. ed. 5. 298. 1754.

Annual, biennial, or perennial herbs [rarely subshrubs], glabrous or most commonly pubescent with unbranched, furcate, dendritic, or stellate trichomes. Stems erect, leafy [or leafless]. Basal leaves petiolate, usually undivided, entire to variously toothed, rarely lyrate-pinnatifid, often forming a distinct rosette. Cauline leaves sessile or rarely petiolate, amplexicaul or sometimes auriculate at base. Inflorescences ebracteate [or bracteate], terminal, corymbose racemes [or panicles], greatly elongated in fruit; fruiting pedicels erect, spreading, or reflexed. Sepals erect, oblong to ovate, equal or unequal, the lateral pair sometimes saccate at base. Petals white, lilac, or purple, rarely light yellow, spatulate to oblanceolate or oblong, rarely obovate, sharply differentiated into claw and blade, sometimes narrowed to a clawlike base, rounded to emarginate at apex. Lateral nectar glands flat, usually ringlike or horseshoe shaped; median glands flat, conical, or toothlike, free or united with the lateral ones, rarely absent. Stamens 6, tetradynamous; filaments linear, neither appendaged nor winged; anthers ovate or oblong to linear, sometimes sagittate at base. Fruits dehiscent, linear, flattened parallel to the septum, rarely slightly 4-angled or subterete, straight or falcate, sessile or stipitate; valves glabrous or pubescent, usually with a distinct midrib [rarely nerveless]; septum membranaceous, complete, not veined; styles persistent, distinct or obsolete; stigmas capitate, entire or slightly 2-lobed. Seeds numerous, orbicular to oblong, compressed or somewhat plump, winged or marginate to wingless, uniseriately or biseriately arranged, nonmucilaginous when wet; cotyledons accumbent. Base chromosome numbers 6–8. (Including *Arabidium* Spach, *Arabisa* Reichenb., *Boechera* Löve &

Löve, *Fourraea* Greuter & Burdet, *Turrita* Wallr., *Turritis* L.[9]) LECTOTYPE SPECIES: *A. alpina* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2**: 178. 1913. (Name after the Arabian region; see Linnaeus, Philos. Bot. 169. 1751. Fournier's derivation of *Arabis* as a defective form of *Draba* is unlikely.)—WALLCRESS, ROCKCRESS.

A well-defined genus of about 180 species distributed in the temperate areas of the Northern Hemisphere north of the 29th parallel. The only exceptions to this range are the circumpolar *Arabis alpina* and *A. glabra* (L.) Bernh., which appear to be native to the high mountains of tropical East Africa (Jonsell). The genus is most highly diversified in North America, where about 60 of the 75 species are endemic to areas west of the 105th meridian. There are about 44 species (30 endemic) in Europe, 31 (20 endemic) in Southwest Asia and the Caucasus, 19 (10 endemic) in central Asia, 28 (22 endemic) in China and the Far East, and 15 (6 endemic) in northwestern Africa (author's compilation). About 75 percent of the species of *Arabis* are perennial, and only about 17 percent are annual or biennial. The remainder are annuals or biennials that sometimes become perennials (author's compilation). Busch listed four central Asiatic species as shrubs, but these are actually subshrubs that have been transferred to genera allied to *Arabis.* The genus is represented in the southeastern United States by ten species, of which all are indigenous and one is endemic.

Schulz's sectional classification of *Arabis,* which is the latest and most comprehensive, is not satisfactory, nor does it represent natural groupings of species. Sixteen sections (five monotypic) were recognized on the basis of characters (e.g., orientation of fruits, saccation of lateral sepals, length of midnerve of valves) that are now considered to be insignificant. The artificiality of Schulz's sections is immediately recognized if the genus is examined on a worldwide basis. Rollins (1941) was fully justified in concluding (p. 294) that "among the western American species of *Arabis* truly natural subdivisions of the genus other than the species themselves are nonexistent." In my opinion, his conclusion may well apply to the genus as a whole.

Arabis glabra (L.) Bernh. (*Turritis glabra* L.; see Rollins (1941) and Burdet (1969) for nine additional synonyms), tower mustard, $2n = 12$, is a circumpolar species with weedy tendencies. It is widespread in most of the temperate parts of North America, Asia, and Europe, where it grows in meadows, open woods, fields, and disturbed sites, on cliffs, bluffs, canyon walls, and rocky places, and along roadsides, railroad embankments, streams, and lake shores. It is distributed in North America from Quebec to Alaska, south to California, and east

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[9] *Arabis* and *Turritis* were simultaneously described by Linnaeus (Sp. Pl. **2**: 664, 666, respectively. 1753). Lamarck (Encycl. Méth. **1**: 218, 219. 1783), who was the first to unite the two genera, adopted *Arabis* for the combined genus, and consequently this name has priority (see ICBN Article 57.2. 1983). Hopkins (p. 64) suggested that Gaudin (Fl. Helvetica **4**: 299. 1829) was the first to unite these genera. However, Lamarck placed the two Linnaean species of *Turritis, T. hirsuta* L. and *T. glabra* L., in the synonymy of two species of *Arabis* and specifically stated that he was merging the former genus with the latter. He indicated (p. 218) that, "les genres de l'*Arabis* & du *Turritis* de Linné n'étant nullement distingués entr eux par leur fructification, & n'ayant pas même les caractères qui leur ont été attribués, se trouvent réunis dans cet article."

through Tennessee (Wayne County) and North Carolina (Avery, Madison, and Watauga counties). Hopkins reported *A. glabra* from Little Rock, Arkansas, but E. B. Smith, apparently overlooking this record, excluded it from the state flora. The species is easily distinguished by its creamy-white to yellowish petals, hirsute stems with usually unbranched trichomes near the base, sagittate-amplexicaul cauline leaves, erect, appressed, subterete fruits 4.5–10 cm long, and numerous, usually biseriately arranged seeds.

A few authors have considered *Arabis glabra* to be a European plant wholly naturalized in North America. As shown by Rollins (1981, family references), however, the species is evidently part of the natural vegetation in numerous parts of the United States and is represented in North America by the widespread var. *glabra* and by the indigenous var. *furcatipilis* M. Hopkins. The latter is endemic to a few widely separated localities in California and Utah. A third variety, var. *pseudoturritis* (Boiss. & Heldr.) Fiori (Italy, Sicily, and the Balkan peninsula), has been treated as a distinct species by most European authors, who cite its winged, uniseriately arranged seeds, longer fruits, and shorter fruiting pedicels in separating it from *A. glabra*. Titz & Schnattinger, however, have demonstrated that these alleged differences have little taxonomic value and that the two taxa have no barriers preventing hybridization.

Arabis hirsuta (L.) Scop. (*Turritis hirsuta* L.), $2n = 32$, another circumpolar species, is represented in North America by four indigenous varieties, two of which occur in the Southeastern States. Varietas *pycnocarpa* (M. Hopkins) Rollins (*A. pycnocarpa* M. Hopkins, *A. ovata* sensu Small (1933); see Rollins (1941) for several additional synonyms), $2n = 32$, is widely distributed from Quebec west into British Columbia and Yukon, south to California, and east into Georgia (Floyd County). It grows in calcareous or sandy soils of cliffs, ledges, hillsides, and woods. The range of var. *adpressipilis* (M. Hopkins) Rollins (*A. pycnocarpa* var. *adpressipilis* M. Hopkins) extends from Missouri to Minnesota, east to Ontario, and south to central Tennessee (Rutherford, Wayne, and Wilson counties) and northern Arkansas (Carroll, Marion, and Washington counties). Gattinger's report of *A. hirsuta* from Tennessee (Cumberland Mtn.) probably should be referred to this variety. The type of pubescence on the stem is very important in distinguishing between these varieties. In var. *pycnocarpa* the trichomes are spreading and unbranched, while in var. *adpressipilis* they are appressed and malpighiaceous. Both varieties differ from the western North American ones, vars. *glabrata* Torrey & A. Gray and *Eschscholtziana* (Andrz.) Rollins, in having white to yellowish petals 3–5 mm long and strictly erect fruits. Rickett's report of *A. hirsuta* from Louisiana is doubtful; I have not seen any specimens from that state.

Titz (1972b) suggested that *Arabis hirsuta* is very likely an allotetraploid, the parents of which are *A. sagittata* (Bertol.) DC. and *A. ciliata* Clairv. (both with $2n = 16$). However, he later (1978b) concluded that this origin is unlikely because of the failure of *A. hirsuta* to cross with the synthetic allotetraploid of these species. *Arabis hirsuta* is easily distinguished from the other species of the genus in the Southeast by its erect, torulose, strongly compressed fruits, its winged, uniseriately arranged seeds, its sagittate cauline leaves, and its creamy-white flowers.

The third species, *Arabis lyrata* L. (*Erysimum lyratum* (L.) Kuntze, *Cardaminopsis lyrata* (L.) Hiitonen), sand cress, $2n = 16, 32$, is widely distributed in eastern Asia and in North America north of the 34th parallel. In the southeastern United States it is common in western North Carolina (disjunct in Jones County) and adjacent eastern Tennessee (disjunct in Davidson County) and is rare in northern Georgia and Mississippi (Lafayette County). It is a biennial or short-lived perennial that grows on sand, sandstone, or limestone. It is distinguished by its lyrate to pinnatifid lower leaves, sessile, nonauriculate cauline leaves, and ascending fruits (0.7–)2–4 cm long.

Arabis canadensis L. (*A. falcata* Michx.), sicklepod, $2n = 14$, grows in rich woods and thickets and on bluffs, rocky banks, and wooded dunes from central Maine west through Ontario to Minnesota and Iowa, south through Nebraska to Texas, and east throughout the Southeastern States. It is widespread in Arkansas, Tennessee, and western North and South Carolina and is sporadic in Georgia (Clarke, Early, Randolph, and Wilkes counties), Florida (Jackson, Liberty), Alabama (Lee, Madison, Tuscaloosa), Mississippi (Jefferson, Lee, Lowndes, Marshall, Noxubee), and Louisiana (Bossier Parish). The species is easily identified by its hirsute, oblong-lanceolate, often denticulate leaves attenuate and nonauriculate at the base, its flat, falcate, pendent or recurved fruits to 3.5 mm wide, and its broadly winged, uniseriately arranged seeds.

Arabis laevigata (Muhl. ex Willd.) Poiret (*Turritis laevigata* Muhl. ex Willd.; see Hopkins for six other synonyms), $2n = 14$, is a glaucous and completely glabrous biennial with undivided basal leaves and dentate to entire, auriculate cauline leaves, white petals scarcely exceeding the sepals, and falcate, recurved fruits 6–12 cm long. Of the two varieties generally recognized in the species, var. *laevigata* is widespread and grows in rich woodlands and river-bank thickets and on slopes and floodplains from Quebec west to South Dakota, south through eastern Colorado, Kansas, and Oklahoma, and east to Alabama and Georgia. It has not been recorded from Florida, Louisiana, or Mississippi and is here first reported for South Carolina (based on *Spongberg, Bozeman, & Logue 67-73*, GH, from McCormick County). Varietas *Burkii* Porter (*A. Burkii* (Porter) Small) grows on dry hillsides and bluffs in Pennsylvania, Maryland, West Virginia, Virginia, North Carolina (Swain and Watauga counties), and Tennessee (Knox County). It has been said to grow in Georgia (Radford *et al.*), but I have not seen any material from this state, and Duncan & Kartesz did not include it in their checklist. Varietas *Burkii* differs from var. *laevigata* in having nonauriculate, usually entire, linear-lanceolate cauline leaves instead of auriculate, usually denticulate, lanceolate to oblong-lanceolate ones.

Hopkins reduced *Arabis serotina* Steele (shale barrens of Virginia and West Virginia) to a synonym of *A. laevigata* var. *Burkii*. However, it differs from both varieties of *A. laevigata* in its lax, profusely branched, paniculate inflorescences, pendent flowers, and straight, pendent fruits, as well as in its late (mid-July through August) flowering. *Arabis laevigata* has racemose inflorescences, ascending flowers, and arcuate fruits, and it flowers early (late April to early June). This evidence supports the recognition of *A. serotina* as a distinct species (Wieboldt).

A very close relative of *Arabis laevigata*, with which it is confused, *A. mis-*

souriensis Greene (*A. viridis* Harger, *A. laevigata* var. *missouriensis* (Greene) Ahles), grows on bluffs and ledges, as well as in fields and sandy or rocky woodlands. It is distributed from Maine west to Wisconsin, south to southern Missouri, western and central Arkansas, and adjacent Oklahoma, and east to Georgia (Kenshaw Mtn., Cobb County), South Carolina (Lancaster County), and North Carolina (Anson, Burke, and Stanley counties). It has not been recorded from the other Southeastern States. *Arabis missouriensis* is distinguished from *A. laevigata* in having subappressed, more numerous, nonglaucous cauline leaves, lyrately pinnatifid basal leaves, petals nearly twice as long as the sepals, and fruit valves with a prominent midvein extending at least to the middle. The latter has fewer (to ca. 13), ascending, glaucous cauline leaves, dentate basal leaves, smaller petals hardly exceeding the sepals, and valves prominently veined only at the base. Hopkins recognized the pubescent forms of *A. missouriensis* (Indiana, Missouri, Wisconsin) as var. *Deamii* M. Hopkins. Although I have not seen adequate material of this taxon, it is doubtful that it merits recognition.

The range of *Arabis patens* Sullivan includes Pennsylvania and Indiana south to North Carolina (Madison County), Tennessee (Jefferson and Knox counties), Alabama (Bibb County), and Mississippi (Noxubee County). It grows in rocky places along creeks and rivers and on limestone on wooded slopes. It is distinguished by its hirsute stems with spreading, mostly unbranched trichomes, auriculate cauline leaves that are hirsute on both sides, saccate sepals, white petals (5–)7–10 mm long, divaricately ascending fruits 2.5–4.5 cm long, and winged seeds.

Arabis georgiana Harper, which is most closely related to *A. patens,* is a narrow endemic of the southeastern United States. It occurs on moist rock and rich alluvium along river banks in Georgia (Gordon, Muscogee, and Stewart counties) and Alabama (Bibb and Elmore counties). It differs from *A. patens* in having longer (6–7 vs. 2.5–4.5 cm) fruits and leaves with stalked, furcate or stellate (instead of simple) trichomes.

The two remaining species of *Arabis* in the Southeast are easily distinguished from the previous ones in having nonsaccate sepals, petals 2–4 mm long, pubescent fruits, and wingless seeds. *Arabis perstellata* E. L. Braun grows on clay loam over limestone in the shade of hardwood forests. It consists of two highly localized varieties. Varietas *perstellata* is known only from wooded hillsides at Elkhorn Creek in Franklin County, Kentucky, while var. *ampla* Rollins ($2n = 14$) is restricted to a calcareous bluff above the Stones River at Percy Priest Lake, northeast of Una, in Davidson County, Tennessee. The former is a densely pubescent plant to only 4 dm tall with basal leaves rarely longer than 4 cm, while var. *ampla* is sparsely pubescent, 4–8 dm tall, and with basal leaves 8–16 cm long.

Arabis Shortii (Fern.) Gleason (*A. perstellata* var. *Shortii* Fern.; *Sisymbrium dentatum* Torrey (1833), non Allioni (1785); *A. dentata* (Torrey) Torrey & A. Gray (1838), non Clairville (1811); *Iodanthus dentatus* (Torrey) Greene), $2n = 12$ (F. H. Smith), grows on limestone bluffs, cliffs, and floodplains, in rich woods, and along streams or riverbanks. It is distributed from New York west to Minnesota and South Dakota, south through Nebraska, Kansas, and Oklahoma, and east to Arkansas (Marion County), Tennessee (Davidson and Montgomery counties), and Alabama (Bibb County). It is very rare and appears to be an endangered species in the Southeast.

All records of *Arabis perstellata* from states other than Kentucky and Tennessee are based on plants of *A. Shortii.* Several authors have recognized glabrous-fruited plants of the latter as *A. Shortii* var. *phalacocarpa* (M. Hopkins) Steyerm. (*A. dentata* var. *phalacocarpa* M. Hopkins, *A. perstellata* var. *phalacocarpa* (M. Hopkins) Fern.). The variety is rare in Iowa and Arkansas (Cleburne, Madison, and Pope counties) but is widespread in Missouri in counties where var. *Shortii* (with pubescent fruits) occurs. It is with some hesitation that I recognize varieties in this species. Field observations may well reveal that both glabrous and pubescent fruits are found in the same population and that no formal subdivisions of the species are needed.

Arabis perstellata is easily distinguished from *A. Shortii* in having pinkish petals 3–4.5 mm long, fruiting pedicels 5–9(–13) mm long, and sessile, stellate trichomes on the leaves. The latter species has creamy-white petals 1.5–2(–3) mm long, fruiting pedicels (1–)1.5–3 mm long, and primarily simple trichomes on the upper leaf surface and short-stalked ones on the lower. A few authors (e.g., Fernald, in family references; Voss) have reduced *A. Shortii* to a variety of *A. perstellata.* However, the morphological differences above are sufficient for recognition of both as distinct species.

Arabis alpina has been reported from Anderson County, Tennessee (Sharp *et al.*), but I have not seen any material from that area, and it is highly unlikely that the species is indigenous to the United States. Hopkins reported *A. alpina* from Greenland, Baffin Island, Labrador, Newfoundland, and Quebec, where it appears to be native.

Arabis is a natural genus characterized by its linear fruits that are almost always flattened parallel to the septum, its accumbent cotyledons, its compressed, usually marginate or winged seeds, its entire to dentate (never pinnatifid) cauline leaves, and its usually branched trichomes. The nearest American relative of *Arabis* is probably *Sibara* Greene, from which it differs in several characters (see *Sibara*). Species of *Arabis* having petiolate cauline leaves and fruit valves with prominent midveins have been transferred to *Cardaminopsis* (C. A. Meyer) Hayek. Although I have not studied this group thoroughly, I concur with Rollins (1941) in retaining the American segregates of *Arabis.*

A few recent European authors (e.g., Burdet, 1967, 1969; Cullen; Dvořák; Hedge) have recently maintained both *Arabis* and *Turritis.* The differences are said to be white to purple flowers, uniseriately arranged seeds, and flattened fruits in *Arabis,* and yellowish flowers, biseriately arranged seeds, and subterete fruits in *Turritis.* These differences, however, readily break down upon careful examination of both genera on a worldwide basis. As was shown by Rollins (1941), all of these differences break down within *A. glabra,* the type species of *Turritis.* Furthermore, *Arabis* and *Turritis* are indistinguishable in seed-coat anatomy, fatty-acid composition, and glucosinolate content. It is quite evident that the latter does not merit recognition.

Löve & Löve have segregated several North American species of *Arabis* as *Boechera* because they have a base chromosome number of seven instead of the eight that is characteristic of the Eurasian species. They and Weber stated that *Boechera* differs from *Arabis* in having entire leaves and clustered caudices, instead of dentate leaves and slender root systems. A casual observation of *Arabis* immediately reveals that these alleged morphological differences are both unrealistic and misleading. I fully agree with Rollins (in Rollins & Rüdenberg, 1977, p. 102) that *Boechera* "has no merit and should not be followed."

Protogyny is apparently more widespread in *Arabis* than was once believed. In addition to the ten protogynous species listed by Al-Shehbaz (1977), there are at least 12 others, of which *A. georgiana, A. laevigata, A. missouriensis, A. patens, A. perstellata,* and *A. Shortii* are reported here for the first time. Earlier observations (e.g., Knuth) of protogyny in *A. glabra* are confirmed by my study of plants growing in Cambridge, Massachusetts. Many species of *Arabis* that are facultatively or predominantly autogamous (e.g., the *A. hirsuta* complex (Titz, 1972b), *A. Holboellii* Hornem. (Johnson)) produce protogynous flowers under favorable conditions.

Böcher's (1951) discovery of agamospermy in diploid and tetraploid plants of *Arabis Holboellii* from Alaska and Greenland was the first record of this type of apomixis for the Cruciferae. He observed several abnormalities in mega- and microsporogenesis (often causing the formation of unreduced nuclei and the development of pollen as monads and dyads), found male nuclei in mature, unfertilized embryo sacs, and reported tetraploid and hexaploid endosperm in diploid and triploid plants, respectively. Johnson did not detect apomixis in *A. Holboellii* from Washington and concluded that his plants were sexual. Apomixis has also been suggested in *A. microphylla* Nutt. and *A. sparsiflora* Nutt. (Böcher, 1969), in *A. divaricarpa* A. Nelson, *A. Drummondii* A. Gray, and *A. Lyallii* S. Watson (Mulligan), and in *A. platysperma* A. Gray var. *platysperma* (Vorobik, 1985). The last author has observed that all of these species have a substantial seed set and very low pollen fertility. Supernumerary chromosomes have been observed in these apomictic species complexes, which are considered to be taxonomically difficult and puzzling. Rollins (1966) suggested that it is very likely that apomixis, hybridization, and polyploidy, whether occurring separately or together, are responsible for creating such highly variable species complexes.

Self-incompatibility has been reported for *Arabis Constancei* Rollins, *A. aculeolata* Greene, *A. modesta* Rollins, and *A. oregana* Rollins (Rollins, 1971; Vorobik, 1985). Polyembryony has been observed in *A. Lyallii* (Lebègue), *A. Halleri* L., and *A. hirsuta* (Miannay). Miannay has suggested that the additional embryos originate from the synergids either by apogamy or by fertilization.

Chromosome numbers have been reported for 84 species. For 44 species (52 percent) the base number is eight, for 34 species (41 percent) seven, and for the remainder six. Burdet (1967) has suggested that the base chromosome number for *Arabis* is four, but as shown by Titz (1968a), his assumption was not well founded. Fifty-five species (65 percent) are diploid, about 16 (ca. 20 percent) are exclusively polyploid, and the remainder have both diploid and polyploid populations. Unlike *Cardamine,* in which about 62 percent of the species are exclusively polyploid, polyploidy has not played a major role in the evolution of *Arabis.*

Mulligan concluded that all species of *Arabis* indigenous to North America have a base chromosome number of seven, whereas the Asiatic and European species are based on eight. Rollins (1966) suspected that this correlation was based on phylogenetic rather than geographic relationships and suggested that in order to verify Mulligan's hypothesis, several North American species with obvious Asiatic relatives should be studied cytologically. Three such species (*A. aculeolata, A. modesta, A. oregana*) are now known to have $x = 8$ (Rollins & Rüdenberg; Vorobik, 1985). Other exceptions to Mulligan's useful correlation are three Old World species, *A. Turczaninowii* Ledeb. (Far East), *A. conringioides* Ball (Morocco), and *A. Brassica* (Leers) Rauschert (central Europe), all of which have $2n = 14$.

Although interspecific hybridization between many pairs of species has been suggested, only a few cases have been subjected to thorough study. Vorobik (1985) concluded that hybridization is uncommon among species of *Arabis* in Oregon and that complex patterns of variability, which have been attributed to hybridization, may have resulted from agamospermy, autogamy, and the colonizing tendencies of several species. Interspecific hybridization among the European members of the *A. hirsuta* complex is very rare and nearly always produces completely sterile hybrids (Novotná & Czapik, 1971, 1974; Titz, 1968a, 1970). Rollins (1983b) reported several cases of sympatry and putative hybridization between *A. Drummondii* and *A. Holboellii* and between the latter and *A. Williamsii* Rollins. He concluded that, due to the uniformity of the parental species and their intermediates and to the lack of hybrid swarms, apomixis probably dominates the reproductive patterns in these complexes. Rollins also suggested that *A. divaricarpa,* which is widely distributed in northern North America, is most likely derived from hybridization between *A. Drummondii* and *A. Holboellii* and that its present uniformity in many parts of its range may have resulted from facultative apomixis. Braun (1940) collected a supposed hybrid (*Braun 2216,* GH!) and its parents, *A. laevigata* and *A. perstellata,* all growing sympatrically at the type locality of the latter species. No further observations have been made on this or other putative hybrids of *Arabis* in the Southeast.

The glucosinolate profiles of at least 12 species of *Arabis* have been determined. Most species have large quantities of high homologues of methylsulfinylalkyl and methylthioalkyl groups. (Al-Shehbaz & Al-Shammary; Daxenbichler *et al.*; Hasapis *et al.*; Kjaer & Gmelin; Kjaer & Schuster; Rodman & Chew). The seeds of about 29 species show two very distinct patterns of fatty-acid composition, the chemotaxonomic value of which is not fully understood (Appelqvist; Mikolajczak *et al.*; Miller *et al.*; Kerber & Buchloh). Twenty-four species (including *A. alpina, A. caucasica* Willd., and the *A. hirsuta* complex) have high concentrations—(30–)40–67 percent—of linolenic acid and no erucic acid or only a trace (very rarely to 5 percent) of it. The remaining five species (including *A. glabra, A. Holboellii,* and *A. laevigata*) have smaller amounts—

18–30(–37) percent—of linoleic acid and higher concentrations (11–39 percent) of erucic acid.

Several species of *Arabis* are ornamentals, the most widely cultivated of which are *A. alpina* (mountain rockcress) and *A. caucasica* (wall rockcress). Many species have weedy tendencies, but none is a serious weed.

References:

Under family references in Al-Shehbaz (Jour. Arnold Arb. **65:** 343–373. 1984), see Baillon; Bentham & Hooker; Berggren; De Candolle (1821, 1824); Fernald; Hasapis *et al.*; Von Hayek; Jonsell (1982); Knights & Berrie; Knuth; Kumar & Tsunoda; Markgraf; Murley; Radford *et al.*; Rickett; Rodman & Chew; Rollins (1981); Schulz; Small; E. B. Smith; and Vaughan & Whitehouse.

Under tribal references see Al-Shehbaz (1977); Al-Shehbaz & Al-Shammary; Appelqvist; Bolkhovskikh *et al.*; Chester; Clewell; Cole; Corbett; Correll & Correll; Daxenbichler *et al.*; Duncan & Kartesz; Ellis *et al.*; Freeman *et al.*; Gattinger; Goldblatt (1981, 1984, 1985); Hebel; Jones (1974, 1975); Kjaer; Litchfield; MacLeod & MacLeod; MacRoberts; Matthews *et al.*; McKinney; Mikolajczak *et al.*; Miller *et al.*; Mohr; Moore; Rollins *et al.*; Sharp *et al.*; Small; Thompson; and Van Horn.

Anderson, L. C. Noteworthy plants from North Florida. Sida **10:** 295–297. 1984. [*A. canadensis* in Jackson and Liberty counties, Florida.]

Artz, L. Notes on *Arabis lyrata* L. Claytonia **4:** 19–21. 1937.

Avetisian, V. E. Characteristics of variation of the form of lateral nectaries in *Arabis caucasica* Willd. (In Russian.) Biol. Zhur. Armen. **32:** 582–585. 1979.

Böcher, T. W. Cytological studies of *Arabis Holboellii.* (Abstr.) Hereditas **33:** 573. 1947. [Greenlandic material has $n = 21 + 1$.]

———. Cytological and embryological studies in the amphi-apomictic *Arabis Holboellii* complex. Danske Vidensk. Selsk. Biol. Skr. **6**(7): 1–59. 1951. [*A. Holboellii* vars. *Holboellii* and *retrofracta*; chromosome numbers, meiotic irregularities, pollen cytology, embryo-sac development, pseudogamy, apomixis, seed sterility, distributions.]

———. Experimental taxonomic studies in the *Arabis Holboellii* complex. Sv. Bot. Tidskr. **48:** 31–44. 1954. [Chromosome numbers, apomixis, putative hybridization, cultivation, new taxa.]

———. Experimental and cytological studies on plant species. IX. Some arctic and montane crucifers. Danske Vidensk. Selsk. Biol. Skr. **14**(7): 1–74. *pls. 1–10.* 1966. [*Arabis,* 3–5.]

———. Further studies in *Arabis Holboellii* and allied species. Bot. Tidsskr. **64:** 141–161. 1969. [Chromosome numbers of several species complexes, aneuploidy, polyploidy, apomixis.]

Boivin, B. Notes on *Arabis.* Am. Midl. Nat. **54:** 510, 511. 1955. [*A. divaricarpa.*]

Braun, E. L. New plants from Kentucky. Rhodora **42:** 47–51. 1940. [*A. perstellata,* sp. nov.; putative hybrid between this and *A. laevigata.*]

———. Growth habits of *Arabis perstellata. Ibid.* **58:** 292–295. 1956. [Differences between *A. perstellata* and *A. Shortii.*]

Burdet, H. M. Contribution à l'étude caryologique des genres *Cardaminopsis, Turritis* et *Arabis* en Europe. Candollea **22:** 107–156. 1967. [Review of previous counts, 110 new counts, correlation between nucleus volume and chromosome numbers, polyploidy; base number for *Arabis* is four.]

———. La détermination des espèces suisses des genres *Arabis, Turritis, Cardaminopsis* et *Arabidopsis. Ibid.* **24:** 63–83. 1969. [Descriptions, synonymy, key.]

Burns, J. L'infructescence de l'*Arabis glabra.* Rev. Oka **30:** 13–15. 1956.*

BUSCH, N. A. *Arabis*. *In:* V. L. KOMAROV & N. A. BUSCH, eds., Fl. USSR **8:** 172–197. 1939. [English translation by R. LAVOOTT, **8:** 130–148. Jerusalem. 1970.]

CULLEN, J. *Arabis*. *In:* P. H. DAVIS, ed., Fl. Turkey **1:** 422–429. 1965. [Seventeen species; *Turritis*, 429, 430.]

CZAPIK, R. Notes on meiosis in *Arabis hirsuta* s. str., *A. sagittata* and their hybrids. Acta Biol. Cracov. Bot. **14:** 11–26. *pls. 3, 4.* 1971. [Chromosome numbers, aneuploidy, polyploidy, pollen sterility.]

———. Embryology of five species of the *Arabis hirsuta* complex. *Ibid.* **17:** 13–25. *pls. 3, 4.* 1974. [*A. Allionii, A. hirsuta, A. Hornungiana, A. planisiliqua, A. sagittata*; meiosis, megasporogenesis, sexuality.]

——— & I. NOVOTNÁ. Cytotaxonomical and genetic problems of the *Arabis hirsuta* complex II. Acta Biol. Cracov. Bot. **12:** 35–56. *pl. 14.* 1969. [Part I in *Ibid.* **10:** 167–183. *pl. 25.* 1967.]

——— & ———. Chromosome numbers of some representatives of the *Arabis hirsuta* complex from Czechoslovakia. Preslia **44:** 1–6. 1972. [*A. hirsuta, A. Hornungiana, A. planisiliqua, A. sagittata.*]

DVOŘÁK, F. A note on the genus *Turritis* L. Österr. Bot. Zeitschr. **114:** 84–87. 1967. [Differences between *Turritis* and *Arabis*.]

——— & V. UHLÍŘOVÁ. Variability of the nectaries of the genus *Turritis*. Österr. Bot. Zeitschr. **114:** 1–3. 1967. [*A. glabra.*]

FARWELL, O. A. *Arabis viridis* var. *heterophylla*. Rhodora **41:** 80. 1939. [Name replaces var. *Deamii*.]

FERNALD, M. L. *Arabis Drummondii* and its eastern relatives. Rhodora **5:** 225–231. 1903.

FOURNIER, P. L'étymologie d'*Arabis*. Bull. Soc. Bot. France **99:** 33, 34. 1952.

GREENE, E. L. Studies in the Cruciferae.—III. 1. Certain species of *Arabis*. Pittonia **4:** 187–198. 1900.

———. Some western species of *Arabis*. Leafl. Bot. Obs. Crit. **2:** 69–83. 1910.

GÜNTHART, A. Beitrag zu einer blütenbiologischen Monographie der Gattung *Arabis*. Biblioth. Bot. **77:** 1–36. *pls. 1, 2.* 1912. [Floral morphology, nectar glands of 23 species, systematic position of *Arabis*, tribal classification of the Cruciferae.]

HARGER, E. B. A new *Arabis*. Rhodora **13:** 37–39. 1911. [*A. viridis*, sp. nov. (= *A. missouriensis*); distribution in New England.]

HARPER, R. M. A new *Arabis* from Georgia. Torreya **3:** 87, 88. 1903. [*A. georgiana*, sp. nov., from Stewart County.]

———. A new station for *Arabis georgiana*. *Ibid.* **4:** 24, 25. 1904. [Gordon County, Georgia.]

———. Supplementary notes on *Acorus* and *Arabis*. *Ibid.* **40:** 196, 197. 1940. [*A. georgiana.*]

HEDBERG, O. Intercontinental crosses in *Arabis alpina* L. Caryologia **15:** 253–260. 1962. [Weak and easily broken sterility barriers between plants of Sweden and Kenya.]

HEDGE, I. *Arabis*. *In:* K. H. RECHINGER, ed., Fl. Iranica **57:** 201–210. 1968. [Eighteen species; *Turritis*, 213, 214.]

HENDERSON, E. S. Perennials for early bloom. Horticulture **49**(11): 38–41. 1971. [*A. alpina*, 40.]

HOPKINS, M. *Arabis* in eastern and central North America. Rhodora **39:** 63–98, 106–148, 155–186. *pls. 457, 458.* 1937. (Reprinted in Contr. Gray Herb. **116** (same pagination + index pp. 187, 188). 1937.) [Treatment of 18 species, descriptions, distributions, key, 31 maps; *A. canadensis, A. georgiana, A. glabra, A. hirsuta* (as *A. pycnocarpa*), *A. laevigata, A. lyrata, A. missouriensis* (as *A. viridis*), *A. patens*, and *A. Shortii* (as *A. dentata*) in the southeastern United States.]

IHARA, K. Mode of local differentiation in *Arabis lyrata* and *A. gemmifera* (Cruciferae) in Japan. Jour. Fac. Sci. Univ. Tokyo Bot. **12:** 1–36. 1976. [Distributions, habitats, variation.]

JOHNSON, T. F. Investigations in the floral biology of the *Arabis Holboellii* complex. vi + 73 pp. Unpubl. M.S. dissertation, Univ. Washington, Seattle. 1970. [*A. Drummondii, A. Holboellii, A. Lyallii, A. sparsiflora*; chromosome numbers, ultraviolet patterns of flowers, protogyny, pollen fertility, intra- and interspecific crosses, insect pollination.]

JONES, B. M. G. Experimental taxonomy of the genus *Arabis*. Unpubl. Ph.D. dissertation, Univ. Leicester, U. K. 1963.*

———. *Arabis*. *In:* T. G. TUTIN *et al.*, eds., Fl. Europaea **1:** 290–294. 1964. [Thirty-five species; *Turritis* reduced to synonymy.]

———. *Arabis*. Pp. 149, 150 *in* C. A. STACE, ed., Hybridization and the flora of the British Isles. London, New York, and San Francisco. 1975. [Putative hybridization between *A. hirsuta* and both *A. alpina* and *A. Brownii.*]

KERBER, E., & G. BUCHLOH. Sinapinvorkommen und Fettsäuremuster bei *Arabis* L., *Turritis* L., *Arabidopsis* (DC.) Heynh. und *Cardaminopsis* (C. A. Meyer) Hayek (Brassicaceae, Cruciferae). (English summary.) Beitr. Biol. Pflanz. **57:** 93–104. 1982. [Fatty acids and sinapin surveyed in 28 (as 39) species of *Arabis.*]

KJAER, A., & R. GMELIN. L(−)-9-methylsulphinylnonyl isothiocyanate, a new mustard oil present as a glucoside (glucoarabin) in *Arabis* species. Acta Chem. Scand. **10:** 1358, 1359. 1956.

——— & S. E. HANSEN. Isothiocyanates XXXI. The distribution of mustard oil glucosides in some *Arabis* species. A chemosystematic approach. Bot. Tidsskr. **54:** 374–378. 1958. [*A. divaricarpa, A. hirsuta, A. Holboellii, Halimolobos mollis.*]

——— & A. SCHUSTER. Glucosinolates in seeds of *Arabis hirsuta* (L.) Scop.: some new, naturally derived isothiocyanates. Acta Chem. Scand. **26:** 8–14. 1972. [Six glucosinolates, five of which not previously reported from a natural source.]

KRAL, R. Additions to some notes on the flora of the Southern States, particularly Alabama and middle Tennessee. Rhodora **78:** 438–456. 1976. [First report of *A. hirsuta* from Tennessee (Rutherford County), 445; see GATTINGER.]

———. A report on some rare, threatened, or endangered forest-related vascular plants of the South. U. S. Dep. Agr. Forest Serv. South. Reg. Tech. Publ. R8–TP2. Vol. 1. x + 718 pp. 1983. [*A. perstellata*; description, distribution, flowering season, distinguishing characters, habitats, associations, 2 maps.]

LEBÈGUE, A. Embryologie des Crucifères: polyembryonie chez l'*Arabis Lyallii* S. Wats. Bull. Soc. Bot. France **95:** 250–252. 1948.

LEHR, J. H. *Arabis lyrata* forma *parvisiliqua* M. Hopkins. Bull. Torrey Bot. Club **89:** 118. 1962.

LÖVE, Å., & D. LÖVE. Nomenclatural notes on Arctic plants. Bot. Not. **128:** 497–523. 1975. [*Boechera* segregated from *Arabis.*]

MIANNAY, N. Embryologie des Crucifères. Polyembryonie chez l'*Arabis hirsuta* Scop. et l'*Arabis Halleri* L. (English summary.) Bull. Soc. Bot. France **118:** 341–344. 1971.

MULLIGAN, G. A. Chromosome numbers of the family Cruciferae. I. Canad. Jour. Bot. **42:** 1509–1519. 1964. [Counts for 13 species of *Arabis*; the North American species have $x = 7$ and many are apomictic, the Asiatic and European species have $x = 8$ and are sexual.]

NAKAI, T. A new attempt to the classification of genus *Arabis* growing in Japan, Korea, Saghaline and the Kuriles. Bot. Mag. Tokyo **32:** 233–248. 1918. [Treatment of 19 species, distributions, key.]

NOVOTNÁ, I. Experimentelle Bearbeitung der Schotenlänge bei *Arabis hirsuta*-Komplex II. (English summary.) Folia Geobot. Phytotax. **3:** 201–216. 1968. [*A. hirsuta, A. planisiliqua, A. sessilifolia*; part I in Preslia **37:** 144–155. 1965.]

——— & R. CZAPIK. Investigations on some hybrids from the *Arabis hirsuta* complex. Folia Geobot. Phytotax. **6:** 419–440. 1971. [*A. hirsuta, A. planisiliqua, A. sagittata*; sterility, morphology, cytology, pollination.]

——— & ———. Studies on the progenies of hybrids from the *A. hirsuta* complex. *Ibid.* **9**: 341–357. 1974.

PARIS, C. D. The genus *Arabis* in Iowa. Proc. Iowa Acad. Sci. **46**: 161–165. 1940. [Eight species; descriptions, distributions, key.]

PRING, M. E. Biological flora of the British Isles. *Arabis stricta* Huds. Jour. Ecol. **49**: 431–437. 1961.

ROGERS, K. E., & F. D. BOWERS. Notes on Tennessee plants. Castanea **34**: 394–397. 1969. [*A. hirsuta* var. *adpressipilis*, 395.]

ROLLINS, R. C. The genus *Arabis* L. in the Pacific Northwest. Res. Stud. State Coll. Washington **4**: 1–52. 1936a. [Twenty-two species; descriptions, distributions, key, 15 figs.]

———. Notes on *Arabis*. Madroño **3**: 359–362. 1936b.

———. A monographic study of *Arabis* in western North America. Rhodora **43**: 289–325, 348–411, 425–481. 1941. (Reprinted in Contr. Gray Herb. **138** (same pagination + index pp. 483–485). 1941.) [Treatment of 53 species growing west of the 100th meridian; descriptions, distributions, keys; generic relatives, species criteria, chromosome numbers of 15 species, 25 maps; 39 new taxa and combinations.]

———. *Arabis perstellata* in Tennessee. *Ibid.* **62**: 242–244. 1960. [*A. perstellata, A. Shortii,* distinguishing characters and distributions of vars. *ampla* (var. nov.) and *perstellata*.]

———. Chromosome numbers of Cruciferae. Contr. Gray Herb. **197**: 43–65. 1966. [*Arabis,* 44, 45.]

———. Protogyny in the Cruciferae and notes on *Arabis* and *Caulanthus*. *Ibid.* **201**: 3–10. 1971. [*A. Constancei,* sp. nov.; self-incompatibility, protogyny.]

———. Purple-flowered *Arabis* of the Pacific Coast of North America. *Ibid.* **204**: 149–154. 1973.

———. Studies on *Arabis* (Cruciferae) of western North America. Syst. Bot. **6**: 55–64. 1981. [Three new species and a new variety; range extensions of several taxa.]

———. Studies on *Arabis* (Cruciferae) of western North America II. Contr. Gray Herb. **212**: 103–114. 1982. [Five new species; distribution and distinguishing characters of several taxa, keys.]

———. Studies in the Cruciferae of western North America. Jour. Arnold Arb. **64**: 491–510. 1983a. [New taxa of *Arabis,* 496–499.]

———. Interspecific hybridization and taxon uniformity in *Arabis* (Cruciferae). Am. Jour. Bot. **70**: 625–634. 1983b. [*A. divaricarpa, A. Drummondii, A. Holboellii, A. Williamsii*; hybrid origin of *A. divaricarpa,* facultative apomixis.]

——— & U. C. BANERJEE. Pollens of the Cruciferae. Publ. Bussey Inst. Harvard Univ. **1979**: 33–64. 1979. [*A. turrita,* 49.]

——— & L. RÜDENBERG. Chromosome numbers of Cruciferae III. Contr. Gray Herb. **207**: 101–116. 1977. [*Arabis,* 101–104.]

SCHWEIDLER, J. H. Die Eiweiss- oder Myrosinzellen der Gattung *Arabis* L. Beih. Bot. Centralbl. **26**: 422–475. 1910. [Localization and forms of myrosin idioblasts, leaf anatomy.]

SMITH, F. H. Some chromosome numbers in the Cruciferae. Am. Jour. Bot. **25**: 220, 221. 1938. [*A. Shortii* (as *A. dentata*), $n = 6$.]

SUTTER, R. D., L. MANSBERG, & J. MOORE. Endangered, threatened, and rare plant species of North Carolina. ASB Bull. **30**: 153–163. 1983. [*A. glabra, A. laevigata* var. *Burkii, A. patens,* 157.]

TITZ, W. Zur Cytologie und Systematik einiger österreichischer *Arabis*-Arten (einschliesslich *Turritis glabra* L.). Ber. Deutsch. Bot. Ges. **79**: 474–488. 1967. [Chromosome numbers of eight species, evaluation of *Turritis*.]

———. Zur Cytotaxonomie von *Arabis hirsuta* agg. (Cruciferae). I. Allgemeine Grundlagen und die Chromosomenzahlen der in Österreich vorkommenden Sippen. (English summary.) Österr. Bot. Zeitschr. **115**: 255–290. 1968a. [Chromosome counts, base number in *Arabis,* interspecific hybridization.]

———. Chromosomenzahlen europäischer *Arabis*-Arten (Cruciferae). (English summary.) Ber. Deutsch. Bot. Ges. **81:** 217–220. 1968b. [Counts for five species, evaluation of *Turritis.*]

———. Zur Cytotaxonomie von *Arabis hirsuta* agg. (Cruciferae). IV. Chromosomenzahlen von *A. sagittata* (Bertol.) DC. und *A. hirsuta* (L.) Scop. s. str. aus Europa. (English summary.) Österr. Bot. Zeitschr. **117:** 195–200. 1969. [Part II. Morphologische Analyse österreichischer Populationen und die Abgrenzung der Sippen. *Ibid.* 21–53; part III. Verbreitung, Standorte und Vergesellschaftung der Sippen in Österreich und phylogenetische Hinweise. *Ibid.* 87–106.]

———. Zur Cytotaxonomie von *Arabis hirsuta* agg. (Cruciferae). V. Artifizielle und natürliche F$_1$-Hybriden sowie deren Cytogenetik. (English summary.) *Ibid.* **118:** 353–390. 1970. [Rarity of natural hybridization, artificial crosses between five species, meiotic irregularities, pollen sterility, seed set in hybrids.]

———. Untersuchungen an *Arabis tenuisiliqua* Rech. f. et Köie im Hinblick auf Abgrenzung und Phylogenie der Gattung *Arabis.* (English summary.) Ann. Naturhist. Mus. Wien **75:** 235–240. 1971a. [Species anomalous in *Arabis* because of terete fruits and incumbent cotyledons.]

———. Chromosomenzahlen, Systematik und Differenzierungsmuster von *Arabis* L. sect. *Lomaspora* DC. emend. O. E. Schulz (Brassicaceae). (English summary.) Ber. Deutsch. Bot. Ges. **84:** 59–70. 1971b.

———. Zur Evolution der Gattung *Arabis* im Alpenraum. (English summary.) *Ibid.* 697–704. 1972a. [Evolution of autogamy in four sections.]

———. Evolution of the *Arabis hirsuta* group in central Europe. Taxon **21:** 121–128. 1972b. [*A. Allionii, A. ciliata, A. hirsuta, A. planisiliqua, A. sagittata*; facultative autogamy, chromosome numbers, reproductive isolation; see Titz, 1978b.]

———. Nomenklatur, Chromosomenzahlen und Evolution von *Arabis auriculata* Lam., *A. nova* Vill. und *A. verna* (L.) R. Br. (Brassicaceae). (English summary.) Österr. Bot. Zeitschr. **121:** 121–131. 1973.

———. Cytosystematic study of the Iberian taxa of the *Arabis hirsuta* group. Feddes Repert. **87:** 493–502. 1976. [Five species; chromosome numbers, morphology, distributions, habitats, and taxonomy.]

———. Notizie critiche sul genere *Arabis* (Brassicaceae) nella flora d'Italia e dei territori confinanti. (English summary.) Giorn. Bot. Ital. **111:** 1–12. 1977. [Sixteen species.]

———. Experimentelle Systematik und Genetik der kahlen Sippen in der *Arabis hirsuta*–Gruppe (Brassicaceae). (English summary.) Bot. Jahrb. **100:** 110–139. 1978a. [Four taxa; chromosome numbers, artificial hybridization, morphology, nomenclature.]

———. Kritisch-experimentelle Untersuchungen zur Resynthetisierbarkeit von *Arabis hirsuta* s. str. (4x) aus *A. sagittata* (2x) und *A. ciliata* (2x). (English summary.) Beitr. Biol. Pflanz. **54:** 443–466. 1978b. [*A. hirsuta* is not the allotetraploid of *A. sagittata* × *A. ciliata,* as was previously suggested; see Titz (1972b).]

———. Die Interfertilitätsbeziehungen europäischer Sippen der *Arabis hirsuta*–Gruppe (Brassicaceae). (English summary.) Pl. Syst. Evol. **131:** 291–310. 1979. [Ten species; hybridization, sterility barriers, cytology of hybrids.]

———. Über die Relevanz des Baues der Schotenscheidewände und anderer Merkmale für die Cruciferensystematik (mit besonderer Berücksichtigung von *Arabis*). (English summary.) Ber. Deutsch. Bot. Ges. **93:** 405–415. 1980. [Cellular pattern of the fruit septum is constant in some species and variable in others. The systematic value of this character is limited to the species level only and is useless for higher taxa.]

——— & R. Schnattinger. Experimentelle und biometrische Untersuchungen über die systematische Relevans von Samen- und Fruchtmerkmalen an *Arabis glabra* var. *glabra* und var. *pseudoturritis* (Brassicaceae). (English summary.) Pl. Syst. Evol. **134:** 269–286. 1980. [*A. pseudoturritis* reduced to a variety of *A. glabra*; chromosome numbers, morphology, crossability, evaluation of *Turritis.*]

Tuzson, J. v. Die Formen der *Arabis hirsuta* (L.) Scop. Ber. Ver. Pflanzengeogr. Syst. Bot. **1919:** 15–44. 1921. [Forty-seven forms recognized, 13 in North America.]

VILLANI, A. Osservazioni sui nettarii de alcune specie di *Arabis*. Nuovo Giorn. Bot. Ital. **19:** 153–166. *pl. 10.* 1912.

VOROBIK, L. A.. Hybridization and reproductive isolation between sympatric *Arabis* (Cruciferae) in southwestern Oregon. xvii + 245 pp. Unpubl. Ph.D. dissertation, Univ. Oregon, Eugene. 1985. [Twelve species; key, morphology, pollen fertility, chromosome numbers, interspecific hybridization, reproductive biology, pollination, palynology, distributions.]

VOSS, E. G. Michigan flora. Part 2. Dicots. xix + 724 pp. Ann Arbor. 1985. [*Arabis*, 289–295.]

WEBER, W. A. New names and combinations, principally in the Rocky Mountain flora—II. Phytologia **51:** 369–376. 1982. [Twelve species of *Arabis* transferred to *Boechera*, 369–371.]

WHITE, P. S. New and noteworthy plants from Great Smoky Mountain National Park, North Carolina and Tennessee. Castanea **47:** 78–83. 1982. [*A. laevigata* var. *Burkii* in Swain County, North Carolina, 79.]

WIEBOLDT, T. F. The shale barren endemic, *Arabis serotina* (Brassicaceae). Sida **12:** 381–389. 1987. [Differences between *A. serotina* and *A. laevigata* var. *Burkii*; distributions, illustrations.]

33. **Sibara** Greene, Pittonia 3: 10. 1896.

Annual or biennial herbs, usually glaucous above, glabrous or with simple, 2-forked, [or branched] trichomes. Stems erect to decumbent, simple or branched at base. Basal and lowermost cauline leaves petiolate, lyrately pinnatifid [to runcinate or pectinate]; lobes several to many, oblong to ovate [or narrowly linear to filiform], entire or dentate. Upper cauline leaves often similar to the basal ones but usually smaller and less divided, not auriculate [or auriculate to sagittate] at base. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit; flowers inconspicuous [or showy]; fruiting pedicels slender [or stout and nearly as wide as the fruit]. Sepals oblong to ovate, purple or green, erect [to spreading], nonsaccate or the inner pair slightly saccate at base, glabrous to sparsely pubescent, membranaceous at margin. Petals white to pinkish [or purple], obtuse [or emarginate] at apex, undifferentiated [or strongly differentiated] into claw and blade. Lateral nectar glands subtending or surrounding the bases of outer stamens; median glands obsolete or absent. Stamens 6, slightly tetradynamous; anthers ovate [to oblong], usually sagittate at base. Fruits linear, torulose [or smooth], flattened parallel to the septum [or terete], subsessile to short stipitate, straight [or arcuate], erect to divaricate [or reflexed]; valves glabrous [or pubescent], obscurely [to prominently] nerved [or nerveless]; septum complete, hyaline; styles obsolete to 1[–5] mm long, conical [cylindrical, or subclavate]; stigmas entire to obscurely 2-lobed. Seeds orbicular [to oblong], compressed [or plump], narrowly winged [or wingless], reticulate, uniseriately arranged, copiously [to only slightly] mucilaginous when wet; cotyledons accumbent [or incumbent]. Base chromosome number 8 [or 7]. (Including *Planodes* Greene.) TYPE SPECIES: *S. angelorum* (S. Watson) Greene. (Name an anagram of *Arabis*.)

A genus of ten species distributed primarily in central Baja California, southeastern California, southwestern Nevada, southern Texas, and central and northeastern Mexico. *Sibara virginica* (L.) Rollins (*Cardamine virginica* L., *Arabis virginica* (L.) Poiret, *Planodes virginicum* (L.) Greene, *C. hirsuta* L. var. *virginica* (L.) Torrey & A. Gray, *C. parviflora* L. subsp. *virginica* (L.) O. E. Schulz, *C. ludoviciana* W. J. Hooker, *A. ludoviciana* (W. J. Hooker) C. A. Meyer), $2n = 16$, is the most widely distributed member of the genus. It is a weed of open areas, pastures, old fields, clearings, waste places, wet woods, and roadsides from southern and central Texas north through central Oklahoma to southeastern Kansas, eastward into Virginia, and southward throughout the Southeastern States. It is disjunct and rare in central and southern California and adjacent Baja California.

Sibara angelorum, S. pectinata (Greene) Greene, *S. laxa* (S. Watson) Greene, and *S. Brandegeana* (Rose) Greene are narrowly endemic to the lower Sonoran zone of central Baja California, where they grow in sandy or rocky areas among shrubs and trees. *Sibara filifolia* (Greene) Greene is endemic to Santa Cruz Island (California), while both *S. rosulata* Rollins and *S. deserti* (M. E. Jones) Rollins are widespread among creosote-bush scrub in the Death and Saline valleys (California) and in Nye County (Nevada). The remaining species, *S. runcinata* (S. Watson) Rollins (southern Texas south into Puebla, Mexico) and *S. mexicana* (S. Watson) Rollins (Guanajuato, Mexico), together with *S. virginica,* form a well-defined group that differs from the other seven species in its winged, instead of wingless, seeds and its runcinate-pinnatifid, instead of pectinate, leaves.

Species of *Sibara* were previously placed in both *Cardamine* and *Arabis.* As shown by Rollins (1941), however, *Sibara* is easily distinguished from *Arabis* in having petiolate, lyrately pinnatifid to pectinate cauline leaves that resemble the basal ones, no median nectar glands, and fruiting pedicels with unexpanded tips. In *Arabis* the cauline leaves are often morphologically different from the basal ones and are not deeply divided, the median nectar glands are usually well developed, and the fruiting pedicels are expanded below the receptacle. *Sibara virginica* is often confused with *C. hirsuta* and *C. parviflora,* but *Cardamine* has elastic dehiscence of the fruits, spiral coiling of the valves, a narrowly winged replum, and wingless seeds.

Chromosome numbers are known for six species, five of which—*S. angelorum, S. laxa, S. runcinata* (including *S. Viereckii* (O. E. Schulz) Rollins), *S. pectinata,* and *S. deserti*—are tetraploid ($x = 7$). The last species was previously considered to have $2n = 26$, but the most recent count (Rollins & Rüdenberg, 1971) suggests that it has $2n = 28$. Counts for *S. virginica* from material collected in Alabama and Tennessee indicate that it is a diploid, with $2n = 16$. More counts are needed to clarify the chromosomal evolution of *Sibara.*

Only *Sibara virginica* has been surveyed for secondary constituents. The seeds contain high concentrations (44 percent) of erucic acid and smaller amounts (12–17 percent) of eicosenoic, linoleic, and oleic acids (Mikolajczak *et al.*). They also contain three mustard-oil glucosides, 2-hydroxy-2-phenylethyl, 7-methylsulfinylheptyl, and 8-methylsulfinyloctyl glucosinolates (Gmelin *et al.*). It has been suggested that the presence of the last two compounds and of their related nitriles in *Sibara* supports the close association of the genus with both *Rorippa* (as *Nasturtium*) and *Arabis* (MacLeod & MacLeod).

Except for *Sibara virginica,* which is weedy throughout its range, the genus has no economic value.

REFERENCES:

Under family references in AL-SHEHBAZ (Jour. Arnold Arb. **65:** 343–373. 1984), see BRITTON & BROWN; MUENSCHER; MURLEY; RADFORD *et al.*; RICKETT; ROLLINS (1966, 1981); ROLLINS & BANERJEE (1979); ROLLINS & RÜDENBERG (1971, 1977); SCHULZ; SMALL; and E. B. SMITH.

Under tribal references see CLEWELL; CORBETT; CORRELL & CORRELL; DUNCAN & KARTESZ; ELLIS *et al.*; GATTINGER; HEBEL; JONES (1975); MACLEOD & MACLEOD; MACROBERTS; MIKOLAJCZAK *et al.*; MOHR; MOORE; PATMAN; ROLLINS *et al.*; SHARP *et al.*; and SMALL. Under references to *Arabis,* see HOPKINS; KERBER & BUCHLOH; and ROLLINS (1941).

BAKER, E. G. Notes on *Cardamine.* Jour. Bot. London **43:** 254–256. 1905. [*S. virginica* (as *Cardamine*).]

GMELIN, R., & A. KJAER. Isoferulic acid choline ester: a new plant constituent. Phytochemistry **9:** 667–669. 1970. [*S. virginica*; 3-hydroxy-4-methoxycinnamic acid.]

———, ———, & A. SCHUSTER. Glucosinolates in seeds of *Sibara virginica* (L.) Rollins: two new glucosinolates. Acta Chem. Scand. **24:** 3031–3037. 1970.

GREENE, E. L. A proposed new genus of Cruciferae. Pittonia **3:** 10–12. 1896. [*Sibara*; six species recognized.]

———. Certain cruciferous types. Leafl. Bot. Obs. Crit. **2:** 219–221. 1912. [The monotypic *Planodes* proposed for *S. virginica.*]

HOWELL, J. T. *Sibara* on Cedros Island. Leafl. West. Bot. **3:** 229. 1943. [*S. pectinata.*]

MUNZ, P. A. A flora of southern California. 1086 pp. Berkeley, Los Angeles, and London. 1974. [*Sibara,* 300, 301.]

ROLLINS, R. C. Generic revisions in the Cruciferae: *Sibara.* Contr. Gray Herb. **165:** 133–143. 1947. [The basic treatment; 11 species recognized.]

———. Species of *Draba, Lesquerella,* and *Sibara* (Cruciferae). *Ibid.* **211:** 107–113. 1982. [*S. grisea,* sp. nov., 112, 113.]

SHREVE, F., & I. L. WIGGINS. Vegetation and flora of the Sonoran Desert. Vol. 1. x + 840 pp. Stanford. 1964. [*Sibara,* 548–550.]

WIGGINS, I. L. Flora of Baja California. viii + 1025 pp. Stanford. 1980. [*Sibara,* 583, 584, *figs. 553, 554.*]

35. **Rorippa** Scopoli, Fl. Carniol. ed. 1. 520. 1760.

Annual, biennial, or rhizomatous perennial herbs, usually of wet or aquatic habitats, glabrous or pubescent, trichomes unbranched, slender or vesicular. Stems erect to prostrate, leafy, sometimes with adventitious roots from the lower nodes. Basal leaves petiolate or rarely subsessile, entire, dentate, sinuate, lyrate, pinnatisect, or pectinate [rarely bi- or tripinnatisect], occasionally auriculate at base, sometimes forming well-developed rosettes; cauline leaves usually resembling the basal ones but progressively smaller upward. Inflorescence an ebracteate [or bracteate], terminal or lateral, few- to many-flowered, corymbose raceme, greatly [or only slightly] elongated in fruit; fruiting pedicels usually with a pair of minute glands at base. Sepals erect to spreading, ovate to oblong or lanceolate, caducous [or persistent], glabrous or pubescent, usually membranaceous at margin; lateral pair not saccate or slightly [to strongly] so at base. Petals pale to bright yellow, sometimes white or lavender, oblong or oblanceolate to broadly spatulate, undifferentiated to sharply differentiated into blade and claw, longer to shorter than sepals, sometimes vestigial or absent. Lateral nectar glands ringlike or horseshoe shaped; median glands a narrow rim, [toothlike,] or absent, sometimes all glands forming a ring subtending bases of filaments. Stamens 6, tetradynamous [rarely 4 (the lateral pair lacking) and equal in length]; filaments linear, free, unappendaged, usually dilated at base; anthers ovate to oblong, sometimes sagittate at base, obtuse or apiculate at apex. Fruits oblong to linear [or globose], terete, dehiscent [very rarely indehiscent], torulose or smooth; valves 2 [rarely 3–6], thin and papery to coriaceous, glabrous or pubescent, obscurely nerved or nerveless; septum membranaceous, complete, with or without a midvein; styles persistent; stigmas capitate, entire or slightly 2-lobed. Seeds several to numerous, uniseriately or biseriately arranged, oblong to ovoid or cordiform, yellow to reddish brown, colliculate to rugose, tuberculate, foveolate, or reticulate, wingless [or rarely narrowly winged], nonmucilaginous [or mucilaginous] when wet; cotyledons accumbent. Base chromosome numbers 5–8, 11, 12. (Including *Baeumerta* Gaertner, Meyer, & Scherb.,[10] *Brachiolobus* All., *Cardaminum* Moench, *Caroli-Gmelina* Gaertner, Meyer, & Scherb., *Clandestinaria* Spach, *Dictyosperma* Regel, *Kardamoglyphos* Schlecht., *Nasturtium* R. Br., *Pirea* T. Durand, *Radicula* Dill. ex Moench,[11] *Sisymbrianthus* Chev., *Tetrapoma* Turcz. ex Fischer & Meyer.) TYPE SPECIES: *Sisymbrium sylvestre* L. = *R. sylvestris* (L.) Besser.[12] (Name a Latinized form of Old Saxon *rorippen,* used for some mustards.)—YELLOW CRESS.

A well-marked genus of about 80 species distributed on all continents except Antarctica. About 23 species are indigenous to North America, ten to South America, 25 to Europe and Asia, 12 to Africa, five to Australia and New Zealand, four to New Guinea, and one to Polynesia. *Rorippa* is represented in the southeastern United States by eight species, three of which are naturalized weeds. The genus has no xerophytic members, and the great majority of its species grow in open, wet or damp, often disturbed habitats, particularly along streams, rivers, ditches, roadsides, and railroad tracks and in lakes, marshes, and swales.

The sectional classification of *Rorippa* has not been treated adequately on a worldwide basis. De Candolle (1821, 1824) recognized three sections, and Schulz (1936), who united *Nasturtium* and *Rorippa* but wrongly chose the later-

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[10] The generic names *Baeumerta, Cardaminum, Dictyosperma,* and *Pirea* are all synonyms of *Nasturtium,* if this is treated as a genus distinct from *Rorippa.* The generic name *Nasturtium* should not be confused with the common English name nasturtium, which is *Tropaeolum majus* L. of the Tropaeolaceae.

[11] *Radicula* was invalidly published when first used by Hill (Brit. Herb. 264. 1756) because "it coincides with the technical term 'radicula' (radicle) and was not accompanied by a specific name in accordance with the binary system of Linnaeus" (ICBN, Article 20.2, Example 2. 1983). Moreover, when the name was later validated by Moench (Meth. 262. 1794), it lacked priority.

[12] Abrams has wrongly designated *Sisymbrium amphibium* L. as the type of *Rorippa.* Scopoli (Fl. Carniol. 520. 1760) recognized a single species (without giving a binomial), cited the exact phraseology of Linnaeus (Sp. Pl. 2: 657. 1753) for *S. sylvestre,* and did not refer to *S. amphibium.* Therefore, *S. sylvestre* is the type species of *Rorippa.*

published *Nasturtium* for the combined genus, recognized six. Two of Schulz's sections are monotypic, and the remaining four are heterogeneous with evidently artificial boundaries. They were defined without a proper consideration of geography. For example, sect. CLANDESTINARIA (Spach) DC. includes several widely disjunct, unrelated species, each of which is indigenous to South America, the West Indies, North America, China, southeastern Asia, or South Africa. As presently delimited, almost all sections of *Rorippa* need careful evaluation of their boundaries, but it is beyond the scope of this flora to do that. Therefore, I am using a few sectional names only to provide a workable framework.

About 50 species of *Rorippa,* including all except two of the North American ones (see below), probably belong to sect. RORIPPA (sect. *Brachylobos* DC., sect. *Sinuatae* Stuckey) (petals yellow; median nectaries usually connate with the larger, lateral ones; fruits linear to oblong or globose; seeds biseriately arranged, reticulate to colliculate). Stuckey (1972) placed six species in sect. SINUATAE, which was said to differ from sect. RORIPPA in having sinuate leaves that form basal rosettes. Differences in these vegetative characters, however, are unreliable, and sect. SINUATAE is an artificial group of doubtful value.

Perhaps the most controversial group is sect. CARDAMINUM (Moench) DC. (*Nasturtium* R. Br.; see footnote 10 for other synonyms) (petals white, median nectaries absent, fruits linear, seeds reticulate, leaves pinnate, lower nodes with adventitious roots). Many European authors recognize the section as a distinct genus, *Nasturtium,* closely related to *Rorippa.* All of the alleged differences that are said to distinguish *Nasturtium* (or sect. CARDAMINUM) from the rest of *Rorippa* break down in various combinations when the latter is carefully studied on a worldwide basis. Numerous species of *Rorippa* indigenous to the Southern Hemisphere, including the South American sect. KARDAMOGLYPHOS (Schlecht.) Martínez-Laborde, have white flowers, median nectaries, and various seed-coat configurations (Al-Shehbaz & Rollins). There are no adequate grounds to support the maintenance of *Nasturtium* as distinct from *Rorippa*; I therefore strongly support its reduction to synonymy.

Two of the five species assigned by Schulz (1936) to sect. CARDAMINUM are North African taxa treated by Maire as subspecies of *Rorippa africana* (J. Br.) Maire. Two others are North American plants now known as *R. Gambellii* (S. Watson) Rollins & Al-Shehbaz (southern California and central Mexico) and *R. floridana* Al-Shehbaz & Rollins (Florida) (see Al-Shehbaz & Rollins for further details). The fifth species, *R. Nasturtium-aquaticum* (L.) Hayek (*Sisymbrium Nasturtium-aquaticum* L., *Nasturtium officinale* R. Br., *Rorippa Nasturtium* (L.) Rusby; see Markgraf and Sprague (1924) for 10 additional synonyms), watercress, sturshum (Small, 1933), $2n = 32$, is a Eurasian cultivated plant and weed naturalized throughout the world. It grows in all of the Southeastern States in quiet or fast-flowing streams, springs, rivers, ditches, brooks, areas of seepage, as well as in swamps, shallow ponds, and pools. Watercress sometimes forms extensive beds, particularly in alkaline waters containing nitrate (Howard, 1976), but only rarely does it grow on wet grounds. All seven of the previously recognized "varieties" of *R. Nasturtium-aquaticum* were based on minor variations in leaf characters, which can be found within the same population or sometimes even on the same plant (Airy Shaw, 1949; Green, 1962).

Britton & Brown and Small (1933) retained *Rorippa Nasturtium-aquaticum* in *Sisymbrium,* where it was initially placed by Linnaeus (Sp. Pl. **2:** 657. 1753), but they treated the genus as monotypic. As shown by Payson, however, Britton & Brown mishandled the lectotypification of *Sisymbrium* by arbitrarily choosing the first of the 16 Linnaean species listed in *Species Plantarum.*

Rorippa floridana Al-Shehbaz & Rollins (*Cardamine curvisiliqua* Shuttelw., *Nasturtium stylosum* Shuttelw. ex O. E. Schulz), coastal watercress (Small, family references), $2n = 32$, is a submersed or floating plant endemic to Florida (Brevard, Citrus, Clay, Collier, Columbia, Dade, Duval, Gilchrist, Hillsborough, Lake, Levy, Manatee, Marion, Seminole, Sumter, Taylor, Volusia, and Wakulla counties). A few authors (e.g., Clewell; Godfrey & Wooten; Rollins, 1978) have recently reported the European *R. microphylla* (Boenn. ex Reichenb.) Hylander (*N. microphyllum* Boenn. ex Reichenb.; see Airy Shaw (1947) and Markgraf for eight additional synonyms), watercress, $2n = 64$, as naturalized in Florida. Al-Shehbaz & Rollins have shown, however, that all of these records are based on plants of *R. floridana* and that there are no authentic records from the Southeastern States for *R. microphylla,* which is only sporadically distributed in North America.

Deeply submersed plants of *Rorippa floridana, R. microphylla,* and *R. Nasturtium-aquaticum* produce simple (instead of pinnately lobed) leaves, which are characteristic of emergent, floating, or shallowly submersed plants. Rollins (1978) has demonstrated that plants of *R. floridana* (as *R. microphylla*) exhibit high phenotypic plasticity and that leaf morphology can be reversed easily from simple to pinnately lobed, or vice versa, by manipulating the depth at which a given plant is grown. Michaelis has indicated that *R. microphylla* can grow at depths of up to 22 feet (6.5 m).

Rorippa Nasturtium-aquaticum is easily distinguished from both *R. floridana* and *R. microphylla* by its biseriately arranged, coarsely reticulate seeds with 25–50(–60) large areolae on each side and its septum that usually has a distinct midvein. The last two species have uniseriately arranged, moderately to minutely reticulate seeds with more than 100 areolae on each side and have a nerveless septum. The differences among these species are further discussed in Al-Shehbaz & Rollins. *Rorippa floridana* differs from *R. microphylla* in having minutely reticulate seeds with 400–500 areolae on each side and in having emergent leaves with a nonauriculate petiole base and one or two pairs of lateral lobes. On the other hand, *R. microphylla* has moderately reticulate seeds with 100–150(–175) areolae on each side and has emergent leaves with a minutely auriculate petiole base and two to six (rarely one) pair(s) of lateral lobes. They also differ in chromosome number: $2n = 32$ in *R. floridana* (Rollins & Rüdenberg) and $2n = 64$ in *R. microphylla.*

It is often difficult to distinguish between *Rorippa microphylla* and *R. Nasturtium-aquaticum* in material without fruits. Howard & Lyon (1950, 1952) indicated that *R. Nasturtium-aquaticum* has introrse anthers and petals ca. 4 mm long, while *R. microphylla* has extrorse anthers and petals ca. 6 mm long.

On the other hand, Green (1955) and Rowson (in Howard & Manton, 1946) observed smaller pollen and a higher stomatal index (15–18 percent, vs. 10–12 percent) in the former species. These differences, however, are much harder to observe than those of the fruiting material. The two species also differ in their chromosome numbers and, as shown below, produce sterile interspecific hybrids.

The Asian *Rorippa indica* (L.) Hiern (*Sisymbrium indicum* L., *R. indica* (L.) Bailey, *Nasturtium indicum* (L.) DC., *N. montanum* Wall. ex J. D. Hooker, *R. montana* (Wall. ex J. D. Hooker) Small, *S. sinapis* Burman f., *N. sinapis* (Burman f.) O. E. Schulz, *R. sinapis* (Burman f.) Ohwi & Hara, *S. atrovirens* Hornem., *N. atrovirens* (Hornem.) DC., *R. atrovirens* (Hornem.) Ohwi & Hara, *N. heterophyllum* Blume, *R. heterophylla* (Blume) Williams, *Radicula heterophylla* (Blume) Small), $2n = 16, 32, 48, 56$, probably reached North America ca. 1900. Uncommon in the United States (Rollins, 1981), it has been collected from several widely separated localities in Mississippi and Louisiana (Darwin *et al.*, Rickett). *Rorippa indica* is highly variable in petal size, fruit length, leaf margin, and chromosome number, but most of this variation is poorly understood. The taxonomy of this complex is evidently confused, and Schulz (1934) has listed more than 40 synonyms in three species (as *N. indicum, N. sinapis,* and *N. montanum*), all of which probably belong to one polymorphic species. In southeastern Asia, where *R. indica* is indigenous, forms with petals (var. *indica*) and without (var. *apetala* (DC.) Hochr.) are known. These were recognized by Stuckey (1972) as *R. indica* and *R. heterophylla,* respectively. It is evident, however, that the presence or absence of petals was overemphasized and that the two forms are otherwise indistinguishable. Plants of this complex naturalized in North America should be called *R. indica* var. *apetala* (Rollins, 1969). They are easily distinguished from the other annual or biennial rorippas by their small flowers with petals lacking or reduced, their spreading fruiting pedicels 1.5–5 mm long, their linear fruits (1–)1.5–3 cm long, their small, reticulate, uniseriately arranged seeds, and their denticulate, simple or lyrately lobed to pinnatisect, nonauriculate leaves.

Rorippa sylvestris (L.) Besser (*Sisymbrium sylvestre* L., *Nasturtium sylvestre* (L.) R. Br., *Radicula sylvestris* (L.) Druce; see Jonsell (1968) for six additional synonyms), yellow cress, creeping yellow cress, $2n = 32, 40, 48$, is a perennial European and western Asiatic weed that became established in North America as early as 1818 (Stuckey, 1966a). It is common in the northeastern United States and southern Canada and is sporadic elsewhere in North America. It has been reported from all of the Southeastern States except South Carolina, Georgia, and Florida, where it is also likely to be found. *Rorippa sylvestris* grows in a wide range of habitats and as a weed is very difficult to eradicate since it is capable of producing new plants from very small fragments of root. It is highly self-incompatible and rarely sets seeds. The species is distinguished from the other crucifers of the Southeast by its perennial habit with adventitious shoots from root runners, its yellow petals usually 3–5.5 mm long, its spreading fruiting pedicels 4–10(–12) mm long, its often aborted fruits (9–22 mm long when bearing seed), and its deeply pinnatisect leaves with four to six pairs of entire to deeply divided lateral lobes.

The four remaining species of *Rorippa* in the southeastern United States are indigenous. *Rorippa sessiliflora* (Nutt. ex Torrey & A. Gray) Hitchc. (*Nasturtium sessiliflorum* Nutt. ex Torrey & A. Gray, *Radicula sessiliflora* (Nutt. ex Torrey & A. Gray) Greene, *N. limosum* Nutt. ex Torrey & A. Gray, *Radicula limosa* (Nutt. ex Torrey & A. Gray) Greene), yellow cress, marsh cress, $2n$ = 16, is distributed throughout all of the Southeastern States, west to central Texas, north to Nebraska, Iowa, and Wisconsin, and east to Virginia. It grows on mud, gravel, or sand along creeks, streams, and rivers, as well as in ponds and wet fields. It is most common in the central United States, particularly in the Mississippi Embayment. *Rorippa sessiliflora* is a glabrous, apetalous annual with small (3–10 × 1.5–3.3 mm), linear fruits borne on pedicels 0.5–1.5 mm long and numerous (ca. 75–100 per locule) foveolate, yellowish brown seeds about 0.5 mm long. Schulz (1936) placed *R. sessiliflora* (as *Nasturtium*) in his highly artificial sect. CLANDESTINARIA, which included no other North American representatives. I support Stuckey's (1972) placement of the species with its relatives of sect. RORIPPA.

Rorippa sinuata (Nutt. ex Torrey & A. Gray) Hitchc. (*Nasturtium sinuatum* Nutt. ex Torrey & A. Gray, *N. trachycarpum* A. Gray, *R. trachycarpa* (A. Gray) Greene, *Radicula sinuata* (Nutt. ex Torrey & A. Gray) Greene, *Radicula trachycarpa* (A. Gray) Rydb.), spreading yellow cress, $2n = 16$, is very rare in the Southeast, where it has been collected from Clay, Crawford, and Pulaski counties, Arkansas (Smith; Stuckey, 1972). It is widely distributed from Missouri north through Illinois to western Wisconsin, and west through all of the Mountain (except Utah), Pacific, and Southwestern states. It is sporadic in Alberta, British Columbia, and Saskatchewan, Canada. *Rorippa sinuata* grows in a wide range of soil types and habitats (see Stuckey, 1972). It is a perennial with vesicular, hemispherical trichomes that become scalelike on pressed specimens. It is easily distinguished from other species with such trichomes by its sinuate to pinnatifid lower leaves, its usually auriculate cauline leaves, its oblong to spatulate petals that are longer (3.5–6 mm long) than the sepals, its divaricate to recurved fruiting pedicels (3.5–)5–12(–15) mm long, and its colliculate seeds. *Rorippa sinuata* is closely related to *R. ramosa* Rollins, from which it differs in several features discussed by Rollins (1961).

Another species with vesicular trichomes is *Rorippa teres* (Michx.) Stuckey (*Cardamine teres* Michx., *Sisymbrium Walteri* Ell., *R. Walteri* (Ell.) Mohr, *N. tanacetifolium* Hooker & Arnott; see Stuckey (1966b) for 14 additional synonyms). Stuckey (1972) recognized two varieties in the species. The first, var. *teres*, is widely distributed on the Atlantic and Gulf Coastal plains from North Carolina to Florida, west to central Texas and is sporadic in scattered localities in Mexico. It has been reported from all of the Southeastern States except Tennessee. Although Mohr stated that it grows in Arkansas and Stuckey (1972) mapped it from the south-central part of the state, I have seen no specimens that support these records. Smith indicated that it is either rare or a waif in Arkansas.

The second variety, var. *Rollinsii* Stuckey, is distributed primarily along the western coast of Mexico and the eastern coast of Honduras and Nicaragua. It differs from var. *teres* in having shallowly foveolate seeds, pubescent fruits, fruiting pedicels with vesicular trichomes, and glabrous lower stems and upper leaf surfaces. In var. *teres* the seeds are deeply foveolate and the fruits and pedicels are glabrous; the lower stems and upper leaf surfaces bear vesicular trichomes (Stuckey, 1972). *Rorippa teres* is closely related to *R. portoricensis* (Sprengel) Stehlé, from which (in addition to other annual rorippas with vesicular trichomes) it differs in having pinnately lobed leaves with dentate or deeply divided lobes, short (1–2 mm) petals equaling or shorter than the sepals, styles 0.5–1.5 mm long, ascending to divaricate fruiting pedicels 1.5–5 mm long, and foveolate seeds.

Stuckey (1972) suggested that perennial habit, long petals exserted from the calyx, long and apiculate anthers, few and large seeds, and long pedicels, fruits, and styles are primitive, while annual habit, short petals included in the calyx (or absent), short and notched anthers, numerous and smaller seeds, and short pedicels, fruits, and styles are advanced. He considered *Rorippa sinuata, R. teres,* and *R. sessiliflora* to be primitive, intermediate, and advanced, respectively.

Rorippa palustris (L.) Besser (*Sisymbrium amphibium* L. *α palustre* L.; see Jonsell (1968) and Stuckey (1972) for 17 additional synonyms), marsh yellow cress, marsh cress, yellow watercress, $2n = 32$, is the most widely distributed species of the genus. It has an almost complete circumpolar distribution: it is native to North America, Asia, and Europe, apparently introduced in Greenland, Central America, and North Africa, and evidently naturalized in South America, the remainder of Africa, Australia, and New Zealand (Jonsell, 1968). Stuckey (1972) mapped the species as occurring in all of the Southeastern States except Mississippi and Alabama, but Jones (1975) reported it from the former, and it is very likely to be found in the latter.

The infraspecific taxonomy of *Rorippa palustris* is more controversial than that of any other *Rorippa*. Jonsell (1968) recognized four subspecies, of which three are indigenous to North America and the fourth is cosmopolitan, whereas Stuckey (1972) recognized four subspecies and 11 varieties in North America alone. The species contains many morphological extremes that are connected with each other by numerous intermediates that show continuous variation in nearly every character. The lack of sharply defined infraspecific taxa in *R. palustris* makes it rather difficult to identify many of the collected specimens satisfactorily. In this highly variable and widely distributed species, the variation should not be ignored, and some formal groups must be recognized. I am only tentatively accepting Jonsell's (1968) four subspecies, which he described (pp. 158, 159) as "indistinctly delimited." Of these, only one grows in the Southeast.

Subspecies *Fernaldiana* (Butt. & Abbe) Jonsell (*R. islandica* (Oeder ex Murray) Borbás var. *Fernaldiana* Butt. & Abbe, *R. islandica* subsp. *Fernaldiana* (Butt. & Abbe) Hultén, *R. palustris* subsp. *glabra* (O. E. Schulz) Stuckey var. *Fernaldiana* (Butt. & Abbe) Stuckey), $2n = 32$, is widespread in the Southeastern States. It is easily distinguished from the other rorippas by its petals 0.8–2 mm long that are subequal to the sepals, its ovoid to oblong fruits 2.5–7 mm long, its fruiting pedicels subequaling the fruits, and its lack of vesicular trichomes. Records of subsp. *hispida* (Desv.) Jonsell (as a variety or a species) from Florida and Louisiana (Fernald), Tennessee (Sharp *et al.*), and North Carolina (Small, 1933) are most likely based on plants of subsp. *Fernaldiana.*

Many authors (e.g., Coode & Cullen; Fernald, 1928; Hedge & Rechinger; Radford *et al.*; Valentine) have reduced *Rorippa palustris* to a synonym of *R. islandica.* Jonsell (1968) and Stuckey (1972), however, have demonstrated that these are closely related, very distinct species and that all records of *R. islandica* from North America represent misidentifications of plants of *R. palustris.* According to Jonsell (1968), *R. islandica* consists of two varieties, of which one, var. *islandica,* is restricted to the Alps, Pyrenees, and European North Atlantic region (Greenland, Iceland, Norway, the British Isles), and the other, var. *Dogadovae* (Tzvelev) Jonsell, is confined to certain river systems of eastern Russia and adjacent Siberia. Plants of *R. islandica* are prostrate diploids ($2n = 16$) with nonauriculate cauline leaves, sepals and petals 1–1.5 mm long, finely colliculate seeds, and fruits two or three times longer than the pedicels. On the other hand, *R. palustris* is an erect tetraploid ($2n = 32$) with auriculate cauline leaves, sepals and petals 1.6–2.6 mm long, coarsely colliculate seeds, and fruits less than twice as long as the pedicels (Jonsell, 1968; Stuckey, 1972). Berggren indicated that the diameter of the seed-coat colliculae is about 65 μm in *R. palustris* and 35 μm in *R. islandica.*

Some plants of *Rorippa palustris* produce unusual fruits with three or four valves together with the normal two-valved ones. The production of four (rarely six) valves, however, is a constant feature of *R. barbareifolia* (DC.) Kitagawa (Alaska, Siberia). Such fruits, which are also found in the unrelated western North American *Tropidocarpum* W. J. Hooker, are very rare and must have evolved independently within the Cruciferae. They have little or no taxonomic value in *Rorippa* (Gerber; Stuckey, 1972).

The Eurasian *Rorippa amphibia* (L.) Besser and the European *R. austriaca* (Crantz) Besser are both naturalized in North America, but neither has been reported from the Southeastern States.

Rorippa has traditionally been associated with *Barbarea, Cardamine,* and *Arabis,* from which it is distinguished by its yellow (sometimes white) flowers, its terete, obscurely nerved, nonelastically dehiscent fruits, and its wingless, colliculate or foveolate to reticulate, usually nonmucilaginous, biseriately (rarely uniseriately) arranged seeds. Von Hayek suggested that *Rorippa* was derived from *Barbarea* and was ancestral to both *Armoracia* and *Cardamine,* while Schulz (1936) associated it with *Sisymbrella* Spach (two species; southwestern Europe and North Africa). The last is distinguished from *Rorippa* in having attenuate fruits and mucilaginous seeds.

The reproductive biology of most species of *Rorippa* is poorly studied. *Rorippa amphibia, R. austriaca,* and *R. sylvestris* are highly self-incompatible perennials that rarely set seeds because they often form "pure" clones by vegetative reproduction. Both *R. microphylla* and *R. Nasturtium-aquaticum* are self-compatible (Howard, 1976). Petals of the latter show high ultraviolet reflectance at the claws and high absorbance at the blades (Horovitz & Cohen). *Rorippa palustris* is autogamous (Jonsell, 1968), and I believe that both *R. indica* and *R. sessiliflora* are highly autogamous because of their small, apetalous flowers.

Chromosome numbers are known for about 30 species; all except five are based on $x = 8$ (author's compilation). Polyploidy, which occurs in about 45 percent of the species, probably played an important role in the evolution of *Rorippa.* Aneuploidy is rare in the genus and occurs in both *R. indica* and *R. benghalensis* (DC.) Hara. The lowest chromosome number, $2n = 10$, has been reported for *R. subumbellata* Rollins (Rollins, 1966), while the highest, $2n = 64$, is known for *R. microphylla.* In *R. amphibia* both diploid and tetraploid plants based on eight are known. The diploid race is not as widely distributed as the tetraploid, and their natural triploid hybrid has been verified (Jonsell, 1968). In *R. sylvestris* ($x = 8$) tetraploid and hexaploid plants, as well as their pentaploid hybrid, have been found in numerous parts of Europe and North America. Mulligan & Munro concluded that the tetraploid race of *R. sylvestris* is more common in Europe (68 percent of the sample) than in North America (20 percent), while the reverse is true for the hexaploid race (65 percent in North America and 29 percent in Europe).

Natural interspecific hybridization between pairs of *Rorippa amphibia, R. austriaca, R. palustris,* and *R. sylvestris* has been documented in all six possible combinations. Their hybrids have been formally recognized and are listed by Stace. Mulligan & Munro have reported a sterile pentaploid hybrid between *R. sylvestris* (hexaploid) and *R. palustris* (tetraploid). A sterile, triploid ($2n = 24$), first-generation hybrid between the last species and *R. barbareifolia* has also been found (Mulligan & Porsild, 1968). Tetraploids of *R. amphibia* and *R. sylvestris* produce fertile hybrids that often introgress with both parents. Their hybrid is widely distributed and has been reported from at least 20 European countries (Stace). Hybridization between *R. amphibia, R. austriaca,* and *R. sylvestris,* all of which are strongly outbreeding perennials, has completely obliterated species boundaries along several river systems in eastern and central Europe. These hybrid complexes persist for many years by vegetative reproduction (Jonsell, 1968).

The hybrid *Rorippa Nasturtium-aquaticum* ($2n = 32$) × *R. microphylla* ($2n = 64$), *R.* ×*sterilis* Airy Shaw, brown cress ($2n = 48$), is widespread in Europe (Stace) but rare in the United States, where it has been reported from New Hampshire, Connecticut, Michigan, and Idaho (Green, 1962). A highly sterile plant with 20 percent "good" pollen of variable size, it reproduces only vegetatively. It has been obtained experimentally by using *R. microphylla* as the ovulate parent but not by the reciprocal cross. The production of 16 bivalents and 16 univalents in this hybrid indicates that *R. microphylla* is an allotetraploid and that *R. Nasturtium-aquaticum* is one of its parents (Howard & Manton, 1946). The second parent of *R. microphylla* is unknown, but a species of *Cardamine* with uniseriate seeds and a chromosome number of $2n = 16$ has been suggested (Howard, 1976; Howard & Manton, 1940, 1946). Interspecific hybridization between *R. floridana* and *R. Nasturtium-aquaticum* has been suggested (Al-Shehbaz & Rollins).

Only *Rorippa Nasturtium-aquaticum* has been thoroughly studied for volatile constituents and for fatty acids. It contains large amounts (80 percent) of 2-phenylethylglucosinolate, smaller amounts of 8-methylthiooctyl (7 percent) and 7-methylthioheptyl (12 percent) glucosinolates, and a trace of benzylglucosinolate (Gil & MacLeod; MacLeod & Islam). Larger and smaller amounts of the first and second compounds, respectively, were also found in *R. microphylla* (Nielsen *et al.*). The occurrence of 7-methylthioheptyl and 8-methylthiooctyl glucosinolates in the genus was said to support its placement in the tribe Arabideae (MacLeod & Islam). A distinct profile of six glucosinolates has been identified in *R. indica* (Hashimoto & Kameoka). Eight South American species that have been surveyed for flavonoids contain only kaempferol and quercetin glycosides. The lack of isorhamnetin in these species is believed to be characteristic of the Arabideae (Carmona & Pero Martínez). The seeds of *R. Nasturtium-aquaticum* contain comparable amounts (20–32 percent) of oleic, linoleic, and erucic acids. The remainder of the genus, however, has not been surveyed for fatty acids.

The presence of calcium-oxalate crystals in the leaves of *Rorippa crystallina* Rollins is unusual. These crystals, which are very rare in the Cruciferae, must have evolved independently since they occur in obviously unrelated genera, such as *Crambe* L., *Sisymbrium* L. (Metcalfe & Chalk), and *Rorippa.*

Small root or stem fragments of *Rorippa amphibia, R. austriaca, R. floridana, R. microphylla, R. Nasturtium-aquaticum,* and *R. sylvestris,* as well as of their hybrids, can easily be transported downstream and are capable of regenerating new plants. Seeds of species that grow on muddy banks can be dispersed over long distances in the mud attached to the feet of birds. The tiny seeds of many species (e.g., *R. sessiliflora*) float on water. The seeds of *R. Nasturtium-aquaticum* sink almost immediately, but a few may float as long as the air film surrounding them is not broken; they germinate readily and do not have any kind of dormancy (Howard & Lyon, 1952).

Watercress, *Rorippa Nasturtium-aquaticum,* is a crop cultivated throughout the world, particularly in Europe and North America; it is used in salads, soups, mixed juices, and casseroles, as well as for a garnish. Correll & Correll stated that the plant is also eaten by deer, ducks, muskrats, and wildfowl. It is rich in vitamin C and has long been valued as an antiscorbutic. Other medicinal uses (e.g., aphrodisiac, depurative, and febrifuge; a remedy for kidney ailments, tuberculosis, asthma, colds, and constipation) that are listed in the old literature are doubtful. *Rorippa indica* is sold in southeastern Asia both as a medicinal plant and as a vegetable (Ochse, Perry). Several species of *Rorippa,* particularly *R. indica, R. palustris,* and *R. sylvestris,* are cosmopolitan weeds. According to Herklots, *R. Nasturtium-aquaticum* has become a noxious weed that chokes some of the waterways in New Zealand. *Rorippa amphibia* is sometimes grown in aquaria (Bailey *et al.*).

REFERENCES:

Under family references in AL-SHEHBAZ (Jour. Arnold Arb. **65**: 343–373. 1984), see BENTHAM & HOOKER; BERGGREN; BRITTON & BROWN; CAIUS; DE CANDOLLE (1821, 1824); CRISP; FERNALD; VON HAYEK; HEDGE & RECHINGER; HEWSON; HOROVITZ & COHEN; JAFRI; JANCHEN; JONSELL (1982); KNUTH; KUMAR & TSUNODA; MAIRE; MARKGRAF; MET-

CALFE & CHALK; MUENSCHER; MUKHERJEE; MURLEY; PERRY; RADFORD *et al.*; RICKETT; ROLLINS (1966, 1981); SCHULZ; SMALL; and E. B. SMITH.

Under tribal references see AL-SHEHBAZ (1977); BEAL; BOLKHOVSKIKH *et al.*; CHESTER; CLEWELL; COLE; CORBETT; CORRELL & CORRELL; DUNCAN & KARTESZ; ELLIS *et al.*; FASSETT; GATTINGER; GODFREY & WOOTEN; GOLDBLATT (1981, 1984, 1985); HEBEL; JONES (1974, 1975); KJAER; LITCHFIELD; MACLEOD & MACLEOD; MACROBERTS; MCKINNEY; MIKOLAJCZAK *et al.*; MOHR; MOORE; NIELSEN *et al.*; PATMAN; PULLEN *et al.*; ROLLINS *et al.*; SHARP *et al.*; SMALL; STACE; and THOMPSON. Under references to *Arabis,* see ROLLINS & RÜDENBERG.

ABRAMS, L. Illustrated flora of the Pacific States. Vol. 2. viii + 635 pp. Stanford. 1944. [*Rorippa,* 276–279.]

AIRY SHAW, H. K. The botanical name of the wild tetraploid watercress. Kew Bull. **2:** 39–46. 1947. [*R. microphylla* is the earlier name for *Nasturtium uniseriatum*; historical account, translation of and comments on Irmisch's paper; see HOWARD & MANTON (1946) and IRMISCH.]

———. Variation and ecology in the British watercress. Pp. 75, 76, *pls. 8–10 in* A. J. WILMOTT, ed., British flowering plants and modern systematic methods. London. 1949. [*R. microphylla, R. Nasturtium-aquaticum.*]

———. A binary name for the hybrid watercress. Watsonia **2:** 73–75. 1951. [*R.* ×*sterilis.*]

ALLARD, H. A. A sterile form of *Rorippa sylvestris* (L.) Bess. Castanea **24:** 50, 51. 1959.

AL-SHEHBAZ, I. A., & R. C. ROLLINS. A reconsideration of *Cardamine curvisiliqua* and *C. Gambellii* as species of *Rorippa* (Cruciferae). Jour. Arnold Arb. **69:** 65–71. 1988. [*R. floridana, R. Gambellii, R. microphylla, R. Nasturtium-aquaticum*; differences, SEMs of seeds.]

BAILEY, L. H., E. Z. BAILEY, & BAILEY HORTORIUM STAFF. Hortus third. xiv + 1290 pp. New York and London. 1976. [*Nasturtium,* 756; *Rorippa,* 974.]

BALLADE, P. Caulogenèse apicale sur les jeunes racines axillaires du cresson (*Nasturtium officinale* R. Br.). (English summary.) Mem. Soc. Bot. France **115:** 250–258. *figs. 5–13.* 1968. [Root and bud formation, kinetin.]

———. Précisions nouvelles sur la caulogenèse apicale des racines axillaires du cresson (*Nasturtium officinale* R. Br.). (English summary.) Planta **92:** 138–145. 1970.

———. Étude expérimentale de l'organogenèse axillaire chez *Nasturtium officinale* R. Br. Comportement de noeuds isolés cultivés in vitro. Compt. Rend. Acad. Sci. Paris, D. **273:** 2079–2082. 1971. [A related paper in *ibid.* **274:** 1282–1285. 1972.]

BELLUE, M. K. Austrian field cress—new and noxious. Bull. Dep. Agr. Calif. **22:** 385, 386. 1933.* [*R. austriaca.*]

BIDDINGTON, N. L., & B. LING. The germination of watercress (*Rorippa Nasturtium-aquaticum*) seeds. I. The effects of age, storage, temperature, light and hormones on germination. Jour. Hort. Sci. **58:** 417–426. 1983. [Part II in *ibid.* 427–433.]

BLEASDALE, J. K. A. The flowering and growth of watercress (*Nasturtium officinale* R. Br.). Jour. Hort. Sci. **39:** 277–283. 1964. [Long-day plant; effect of day length on stem elongation and branching.]

BLOM, C. En för sveriges flora ny hybrid, *Rorippa austriaca* (Crantz) Bess. × *silvestris* (L.) Bess. Acta Horti Gothob. **6:** 145–150. 1931.

BORBÁS, V. *Rorippa anceps* und *R. Sonderi.* Österr. Bot. Zeitschr. **32:** 42–44. 1882. [Interspecific hybridization.]

BRADLEY, L. J. *Rorippa amphibia* in Fairfield County, Connecticut. Rhodora **33:** 192, 193. 1931.

BRITTON, C. E. A *Radicula*-hybrid. Jour. Bot. London **47:** 430. 1909. [*R. amphibia* × *R. palustris.*]

BUTTERS, F. K., & E. C. ABBE. The American varieties of *Rorippa islandica.* Rhodora **42:** 25–32. *pl. 588.* 1940. [*R. palustris* (as *islandica*); new combinations; var. *Fernaldiana,* var. nov.]

CARMONA, C., & M. A. DEL PERO MARTÍNEZ. Flavonoides en las especies argentinas de *Rorippa* (Cruciferae, Arabideae). (English summary.) Parodiana **3:** 249–268. 1985. [Distribution of 26 leaf flavonoids in eight species.]

CHAMPAGNAT, M., P. BALLADE, & J. PORTE. Introduction à l'étude expérimentale de l'organogenèse axillaire du cresson (*Nasturtium officinale* R. Br.). Mém. Soc. Bot. France **114:** 109–118. 1967.

——— & S. BLATTERON. Ontogénie des organes axillaires du cresson (*Nasturtium officinale* R. Br.). Revue Gén. Bot. **73:** 85–102. 1966. [Anatomy and cytology of adventitious roots; initiation from subepidermis of leaf axils.]

COODE, M. J. E., & J. CULLEN. *Rorippa. In:* P. H. DAVIS, ed., Fl. Turkey **1:** 431–433. 1965.

CURRAN, P. L. *Rorippa sylvestris* (L.) Besser; a weed on cultivated bog. Irish Nat. Jour. **21:** 296–298. 1984.

DARWIN, S. P., E. G. SUNDELL, & A. S. BRADBURN. Noteworthy vascular plants from Louisiana. Sida **9:** 70–75. 1981. [*R. indica* (as *heterophylla*) from Orleans and Rapides parishes, 72.]

DOROFEYEV, V. I. Chromosome numbers in some species of the genus *Rorippa* (Brassicaceae). (In Russian.) Bot. Zhur. **7:** 1142. 1982. [*R. amphibia, R.* ×*anceps, R. austriaca, R. palustris, R. sylvestris.*]

ERDTMAN, G. Über die Pollenmorphologie von *Rorippa silvestris.* Flora **146:** 408–411. 1958.

FERNALD, M. L. *Rorippa islandica* and *R. hispida.* Rhodora **30:** 131–133. 1928. [Synonymy, distributions; *R. palustris* reduced to synonymy of *R. islandica.*]

———. *Rorippa islandica* an invalid name. *Ibid.* **31:** 17, 18. 1929. [*R. palustris* replaces *R. islandica.*]

———. Some spermatophytes of eastern North America. *Ibid.* **42:** 239–276, 281–302. *pls. 598–625.* 1940. [The eastern American varieties of *R. islandica,* 267–274, *pl. 605.*]

———. *Rorippa*: a correction. *Ibid.* **50:** 100. 1948. [*R. palustris* (as *islandica*) var. *Fernaldiana* replaces var. *microcarpa*; see FERNALD (1940).]

FREEMAN, G. G., & N. MOSSADEGHI. Studies on sulphur nutrition and flavour production in watercress (*Rorippa Nasturtium-aquaticum* (L.) Hayek). Jour. Hort. Sci. **47:** 375–387. 1972. [A related paper in *ibid.* **48:** 365–378. 1973.]

FRÖHLICH, A. Über den Bastard *Rorippa austriaca* × *silvestris* und dessen Vorkommen in Mähren. Österr. Bot. Zeitschr. **64:** 120–134. 1914.

GADELLA, T. W. J. *Rorippa palustris* (L.) Besser in the Netherlands. (In German; English summary.) Gorteria **8:** 172–177. 1977. [*R. amphibia, R. islandica, R. palustris, R. sylvestris.*]

GARNOCK-JONES, P. J. *Rorippa* (Cruciferae, Arabideae) in New Zealand. New Zealand Jour. Bot. **16:** 119–122. 1978. [*R. amphibia, R. gigantea, R. palustris, R. sylvestris*; key, maps.]

GERBER, C. Le genre *Tetrapoma,* sa signification. Compt. Rend. Hebdom. Séances Mém. Soc. Biol. Paris, XI. **51:** 665–667. 1899. [*R. barbareifolia, R. palustris*; evaluation of 4-valved fruits.]

GIL, V., & A. J. MACLEOD. Degradation of glucosinolates of *Nasturtium officinale* seeds. Phytochemistry **19:** 1657–1660. 1980.

GREEN, P. S. Pollen grain size in *Nasturtium* and *Cakile.* Trans. Bot. Soc. Edinb. **36:** 289–304. 1955. [Pollen of *R. microphylla* is larger than that of *R. Nasturtium-aquaticum.*]

———. Watercress in the New World. Rhodora **64:** 32–43. 1962. [*R. microphylla, R. Nasturtium-aquaticum,* and their hybrid; distributions, distinguishing characters.]

GREENE, E. L. The genus *Radicula.* Leafl. Bot. Obs. Crit. **1:** 113, 114. 1905. [Enumeration of the North American species.]

GROH, H. Some recently noticed mustards. Sci. Agr. **13:** 722–727. 1933. [*R. amphibia, R. austriaca, R. sylvestris,* 225, 226.]

———. Creeping yellow cress, a weed in process of entrenchment. *Ibid.* **16:** 331–334. 1936. [*R. austriaca, R. palustris, R. sylvestris.*]

Halket, A. C. A note on the occurrence of abnormal flowers of *Nasturtium officinale* R. Br. New Phytol. **31:** 284–286. 1932.

Hansen, A. A. Austrian field cress: a new weed in the United States. Torreya **22:** 73–77. 1922. [*R. austriaca.*]

Harms, V. L., J. H. Hudson, & G. F. Ledingham. *Rorippa truncata,* the blunt-fruited yellow cress, new for Canada, and *R. tenerrima,* the slender yellow cress, in southern Saskatchewan and Alberta. Canad. Field-Nat. **100:** 45–51. 1986. [Diagnostic characters, distributions, maps.]

Harris, S. K. *Rorippa sessiliflora* in Essex County, Massachusetts. Rhodora **60:** 260, 261. 1958.

Hashimoto, S., & H. Kameoka. Sulfur- and nitrogen-containing neutral volatile components of Cruciferae. Jour. Food Sci. **50:** 847, 848, 852. 1986. [*R. indica* contains six glucosinolates.]

Herklots, G. A. C. Vegetables in South-east Asia. xii + 525 pp. New York. 1972. [*R. Nasturtium-aquaticum,* 143–148.]

Høiland, K. *Rorippa islandica,* a threatened species with interesting distribution in the North Atlantic area. (In Norwegian; English summary.) Blyttia **44:** 103–112. 1986. [Morphology, distribution, habitats, differences between *R. islandica* and *R. palustris.*]

Howard, H. W. Chromosome number of *Rorippa* (*Nasturtium*) *sylvestris.* Nature **158:** 666. 1946. [$n = 24$, $2n = 48$.]

———. Wild and cultivated watercress types. Jour. Min. Agr. London **53:** 453–456. 1947a. [*R. microphylla* (as *Nasturtium uniseriatum*), *R. Nasturtium-aquaticum,* and their hybrid; distinguishing characteristics, chromosome numbers, cultivars.]

———. Seed size in crosses between diploid and autotetraploid *Nasturtium officinale* and allotetraploid *N. uniseriatum.* Jour. Genet. **48:** 111–118. 1947b. [The cross *R. microphylla* (as *N. uniseriatum*) × *R. Nasturtium-aquaticum* is successful when the former is used as the ovulate plant.]

———. Chromosome numbers of British species of the genus *Rorippa* Scop. (part of the genus *Nasturtium* R. Br.). Nature **159:** 66. 1947c. [*R. amphibia, R. austriaca, R.* ×*erythrocaulis, R. islandica, R. sylvestris.*]

———. The so-called chromosome-races of *Cardamine pratensis* and *Nasturtium officinale. Ibid.* **168:** 477, 478. 1951.

———. Autotetraploid green watercress. Jour. Hort. Sci. **27:** 273–277. 1952.*

———. Induced and natural polyploidy in *Nasturtium* and *Rorippa.* Pp. 331, 332 *in* Proc. 7th Internatl. Bot. Congr. Stockholm. 1953.

———. Watercress: *Rorippa Nasturtium-aquaticum* (Cruciferae). Pp. 62–64 *in* N. W. Simmonds, ed., Evolution of crop plants. London and New York. 1976. [Cytotaxonomy, early and recent history, prospects.]

——— & A. G. Lyon. The identification and distribution of the British watercress species. Watsonia **1:** 228–233. *fig. 1.* 1950. [Distributions and distinguishing characters of *R. microphylla, R. Nasturtium-aquaticum,* and their hybrid.]

——— & ———. Distribution of the British watercress species. *Ibid.* **2:** 91, 92. 1951a. [Supplementary distributional records.]

——— & ———. Effect of light on the germination of watercress seeds. Nature **168:** 253, 254. 1951b. [*R. microphylla, R. Nasturtium-aquaticum,* and their hybrid.]

——— & ———. Biological flora of the British Isles: *Nasturtium.* Jour. Ecol. **40:** 228–245. 1952. [*R. Nasturtium-aquaticum,* 228–238, *R. microphylla,* 239–245; distributions, habitats, morphology, phenology, reproductive biology, parasites, history.]

——— & I. Manton. Allotetraploid nature of the wild tetraploid watercress. Nature **146:** 303. 1940. [Allotetraploidy between *R. Nasturtium-aquaticum* and probably a species of *Cardamine.*]

——— & ———. Autopolyploid and allopolyploid watercress with the description of a new species. Ann. Bot. II. **10:** 1–13. *pl. 1.* 1946. [Meiosis, artificial and natural hybrids; *Nasturtium uniseriatum,* sp. nov. (= *R. microphylla*); see Airy Shaw (1947).]

Hylander, N. *Rorippa microphylla* i Sverige och Danmark. (English summary.) Bot. Not. **1950:** 1–13. *pls. 1–5.* 1950. [*R. microphylla* is very common in Denmark and rare in Sweden; the reverse is true for *R. Nasturtium-aquaticum.*]

———. *Rorippa amphibia* × *islandica* funnen i norra Finland. (English summary.) Mem. Soc. Fauna Fl. Fenn. **37:** 253–255. 1961.

Irmisch, T. Ueber zwei Varietäten der Brunnenkresse. Bot. Zeit. **19:** 316–319. 1861. [English translation by Airy Shaw (1947).]

Javůrková-Kratochvílová, V., & P. Tomšovic. Chromosome study of the genus *Rorippa* Scop. em. Reichenb. in Czechoslovakia. Preslia **44:** 140–156. 1972. [*R. amphibia, R. austriaca, R. palustris, R. pyrenaica, R. sylvestris,* hybrids.]

Jonsell, B. On *Rorippa* ×*sterilis* in Sweden. Bot. Not. **116:** 1–6. 1963. [Morphology, chromosome numbers.]

———. Chromosome numbers of *Rorippa silvestris* (L.) Bess. in Scandinavia. Sv. Bot. Tidskr. **58:** 204–208. 1964. [Tetra-, penta-, and hexaploid populations based on $x = 8$.]

———. Studies in the North-west European species of *Rorippa* s. str. Symb. Bot. Upsal. **19**(2): 1–221. *pls. 1–11.* 1968. [*R. amphibia, R. austriaca, R. islandica, R. palustris, R. sylvestris*; excellent accounts of intraspecific variation, cytology, and natural and artificial hybridization; reproductive biology and dispersal, palynology, distributions, nomenclature, taxonomy.]

———. *Rorippa islandica* und *R. palustris*—zwei scharf getrennte Arten der Alpenländerflora. Ber. Geobot. Inst. Eidg. Rübel **39:** 52–55. 1969. [Distinguishing characters of both species.]

———. The genus *Rorippa* (Cruciferae) in eastern Siberia and the Soviet Far East. Sv. Bot. Tidskr. **65:** 293–307. 1971. [*R. amphibia, R. barbareifolia, R. globosa, R. microsperma, R. palustris*; status of *R. hispida*; variation, nomenclature, distinguishing characters, key, distributions.]

———. Taxonomy and distribution of *Rorippa* (Cruciferae) in the southern U.S.S.R. *Ibid.* **67:** 281–302. 1973. [Ten species; interspecific hybrids, key.]

———. The genus *Rorippa* (Cruciferae) in tropical Africa and Madagascar. *Ibid.* **68:** 377–396. 1974. [Key, descriptions, synonymy, distributions, chromosome numbers, new combinations.]

———. Hybridization in yellow-flowered European *Rorippa* species. Pp. 101–110 *in* S. M. Walters & C. J. King, eds., European floristic and taxonomic studies. Faringdon, England. 1975. [*R. amphibia, R. austriaca, R. palustris, R. sylvestris*; natural and artificial hybridization, cytogenetics and ecology of hybrids.]

———. New taxa of Cruciferae from East Tropical Africa and Madagascar. Bot. Not. **132:** 521–535. 1979. [*Rorippa,* 531–535.]

———. Släktet *Rorippa* i Norge. (English summary.) Blyttia **45:** 25–29. 1987. [Distinguishing characters and distributions of six species in Norway, key.]

Kaoulla, N., A. J. MacLeod, & V. Gil. Investigation of *Brassica oleracea* and *Nasturtium officinale* seeds for the presence of epithiospecifier protein. Phytochemistry **19:** 1053–1056. 1980. [*R. Nasturtium-aquaticum*; glucosinolates.]

Kaskey, J. B., & D. R. Tindall. Physiological aspects of growth and heteroblastic development of *Nasturtium officinale* under natural conditions. Aquatic Bot. **7:** 209–229. 1979. [Changes of sugar, starch, protein, and chlorophyll contents during various developmental stages of leaves, stems, and roots; variation in photoperiodism, flowering, and leaf morphology.]

Lakela, O. A prostrate *Rorippa* in the interior. Rhodora **50:** 132. 1948. [*R. palustris* (as *islandica*) var. *Fernaldiana* in Minnesota.]

LAWALRÉE, A. Le *Rorippa microphylla* en France. Bull. Soc. Bot. France **97:** 212, 213. 1950. [*R. microphylla, R. Nasturtium-aquaticum*; key, distributions.]

———. L'hybride *Rorippa amphibia* × *R. sylvestris* en Belgique. (English summary.) Gorteria **5:** 170, 171. 1971. [*R.* ×*anceps*; key to hybrid and parental species.]

LYON, A. G., & H. W. HOWARD. Science and watercress growing. Jour. Min. Agr. London **59:** 123–128. 1952.*

MACKENZIE, K. K. The generic name *Radicula*. Rhodora **31:** 119. 1929. [Argument for using *Radicula* instead of *Rorippa*.]

MACLEOD, A. J., & R. ISLAM. Volatile flavour components of watercress. Jour. Sci. Food Agr. **26:** 1545–1550. 1975. [*R. Nasturtium-aquaticum*; major flavoring principles are nitriles derived from glucosinolates.]

——— & G. MACLEOD. Synthesis and natural occurrence of 8-methylthiooctanonitrile and 9-methylthiononanonitrile. Phytochemistry **16:** 907–909. 1977. [*R. Nasturtium-aquaticum*; chemotaxonomic value.]

MANTON, I. The cytological history of watercress (*Nasturtium officinale* R. Br.). Zeitschr. Indukt. Abst. Vererbungslehre **69:** 132–157. *pls. 1, 2.* 1935. [Cytogeography of *R. Nasturtium-aquaticum, R. microphylla,* and their hybrid (all treated as *N. officinale*).]

MARIE-VICTORIN, F. Le genre *Rorippa* dans le Québec. Contr. Lab. Bot. Univ. Montréal **17:** 1–17. 1930. [*R. amphibia, R. palustris, R. sylvestris.*]

MARTÍNEZ-LABORDE, J. B. Novedades en el género *Rorippa* (Cruciferae): una nueva sección y una nueva especie sudamericanas. (English summary.) Parodiana **2:** 67–78. 1983. [*Kardamoglyphos* reduced to a section with two species; key, descriptions, distributions, illustrations, map.]

———. Sinopsis preliminar del género *Rorippa* (Cruciferae) en la Argentina. (English summary.) *Ibid.* **3:** 269–305. 1985. [Eight indigenous and four adventive species; key, distributions, illustrations.]

MICHAELIS, F. B. Watercress (*Nasturtium microphyllum* (Boenn.) Rchb. and *N. officinale*) in New Zealand cold springs. Aquatic Bot. **2:** 317–325. 1976.

MORINAGA, T. Germination of seeds under water. Am. Jour. Bot. **13:** 126–140. 1926. [*R. Nasturtium-aquaticum,* 138, 139.]

MULLIGAN, G. A., & D. B. MUNRO. Chromosome numbers and sexual compatibility in North America of *Rorippa sylvestris* (Cruciferae). Canad. Jour. Bot. **62:** 575–580. 1984. [Chromosome numbers of 74 clones; self-incompatibility, distribution, interspecific hybridization.]

——— & A. E. PORSILD. *Rorippa calycina* in the Northwest Territories. Canad. Jour. Bot. **44:** 1105, 1106. 1966.

——— & ———. A natural first-generation hybrid between *Rorippa barbareaefolia* and *R. islandica*. *Ibid.* **46:** 1079–1081. 1968. [The triploid hybrids ($2n = 24$) are derived from *R. barbareifolia* ($2n = 16$) and *R. palustris* (as *R. islandica*) ($2n = 32$).]

NORTON, A. H. *Rorippa amphibia* in Androscoggin County, Maine. Rhodora **35:** 262. 1933.

OCHSE, J. J. Vegetables of the Dutch East Indies. xxxvi + 1005 + 11 unnumbered pp. Amsterdam. 1977. [*R. indica* (as *Nasturtium heterophyllum*), 175.]

OEFELEIN, H. Die Brunnenkressearten der Schweiz. Bull. Soc. Bot. Suisse **68:** 249–253. 1958.

PAMMEL, L. H., C. M. KING, & A. HAYDEN. Marsh cress, its geography and ecology in Iowa. Proc. Iowa Acad. Sci. **35:** 157–167. 1930. [*R. palustris.*]

PAYSON, E. B. Species of *Sisymbrium* native to America north of Mexico. Univ. Wyoming Publ. Sci. Bot. **1:** 1–27. 1922. [*R. Nasturtium-aquaticum* must not be considered as the type species of a monotypic *Sisymbrium*; see BRITTON & BROWN.]

PROJETTI, M.-L., & D. CHRIQUI. Totipotence du péricycle des organes souterrains et aériens de *Rorippa sylvestris*. I. Rhizogenèse et caulogenèse à partir de racines sur plante intacte ou de fragments de racines cultivés in vitro. Canad. Jour. Bot. **64:** 1760–1769. 1986. [Part II in *ibid.* 1770–1777; effects of auxins and kinetin on initiation of roots and formation of adventitious buds from excised leaves and root fragments grown on culture media.]

RADICS, F. The identification of *Rorippa* species and hybrids (Cruciferae) based on external morphological features of their seeds. Stud. Bot. Hungarica **12:** 55–69. *pls. 1–4, table.* 1977. [*R. amphibia, R. austriaca, R. palustris, R. prolifera, R. pyrenaica, R. sylvestris.*]

RANDALL, R. E. *Rorippa islandica* (Oeder) Borbás sensu stricto in the British Isles. Watsonia **10:** 80–82. 1974. [Distribution, dispersal.]

RHODE, M. C., & W. T. BARKER. Taxonomy and distribution of the genus *Rorippa* (Brassicaceae) in the Great Plains. Proc. N. Dakota Acad. Sci. **34:** 2. 1980. [Seven indigenous and two naturalized species.]

ROLLINS, R. C. The American Cruciferae of Sessé and Mociño. Rhodora **62:** 11–20. 1960. [*R. Gambellii* (as *Nasturtium*), 15; *Rorippa,* 16–19.]

———. Notes on American *Rorippa* (Cruciferae). *Ibid.* **63:** 1–10. 1961. [*R. portoricensis, R. ramosa* (sp. nov.), *R. sinuata, R. teres* (as *R. Walteri*); typification, distributions.]

———. A new crucifer from the Great Slave Lake area of Canada. *Ibid.* **64:** 324–327. 1962. [*R. crystallina,* sp. nov.]

———. On a weed species of *Rorippa. Ibid.* **71:** 552, 553. 1969. [*R. indica* var. *apetala.*]

———. Watercress in Florida. *Ibid.* **80:** 147–153. 1978. [Field and greenhouse observations, variation in leaf morphology; *Cardamine curvisiliqua* reduced to a synonym of *R. microphylla* (as *Nasturtium*); see AL-SHEHBAZ & ROLLINS.]

RÖNNING, O. I. *Rorippa alpina* (S. Wats.) Rydb. in the Rocky Mountains, U.S.A. Norwegian Jour. Bot. **19:** 61–66. 1972.

SCANNELL, M. J. P. *Rorippa islandica* (Oeder ex Murray) Borbás in Ireland. Irish Nat. Jour. **17:** 348, 349. 1973. [Distinguishing characters of *R. islandica* and *R. palustris.*]

SCAVONE, O., & S. PANIZZA. About the morphology and anatomy of *Nasturtium officinale* R. Brown. (In Portuguese; English summary.) Bol. Bot. São Paulo **1:** 117–148. 1973. [Anatomy of root, stem, leaf, flower, fruit, and seed.]

SCHULZ, O. E. Die bisher bekannten Cruciferen Papuasiens. Bot. Jahrb. **55:** 266–272. 1918. [Four new species of *Nasturtium* and one of *Cardamine.*]

———. Beiträge zur Kenntnis der Gattung *Nasturtium* R. Br. I. Repert. Sp. Nov. **33:** 273–285. 1934. [Treatment of nine south African, South American, and southeastern Asian species (including *R. indica*). Part II in *ibid.* **34:** 131–136. 1933; treatment of six North American species. A related paper on three Manchurian and tropical African species in *ibid.* **34:** 137, 138. 1933.]

SHAPIRO, A. M. The role of watercress, *Nasturtium officinale,* as a host of native and introduced pierid butterflies in California. Jour. Res. Lepid. **14:** 158–168. 1975.

SOLDANO, A. *Nasturtium microphyllum* (Boenn.) Reichenb. (Cruciferae) in Italia. (English summary.) Giorn. Bot. Ital. **111:** 109–112. 1977. [Sympatry of *R. microphylla, R. Nasturtium-aquaticum,* and their hybrid.]

SPENCE, R.-M. M., O. G. TUCKNOTT, E. A. BAKER, & P. J. HOLLOWAY. Compounds associated with the surface lipid layer of watercress. Phytochemistry **22:** 1753–1756. 1983. [Numerous volatile and nonvolatile compounds identified from waxes of leaves, stems, and flowers; a related paper in *ibid.* 2521–2523.]

SPRAGUE, T. A. The botanical name of water-cress. Jour. Bot. London **62:** 225–228. 1924. [Synonymy, conservation of the generic name *Nasturtium,* causes of nomenclatural instability.]

———. The source of the generic name *Rorippa. Ibid.* **68:** 219, 220. 1930.

———. *Rorippa islandica* (Oeder) Borbás. *Ibid.* **77:** 343–345. 1939.

STUCKEY, R. L. The distribution of *Rorippa sylvestris* (Cruciferae) in North America. Sida **2:** 361–376. 1966a. [History of introduction, distribution, map.]

———. *Rorippa Walteri* and *R. obtusa* synonyms of *R. teres* (Cruciferae). *Ibid.* 409–418. 1966b. [Nomenclatural history, differences between *R. teres* and *R. truncata.*]

———. Differences in habitats and associates of the varieties of *Rorippa islandica* in the Douglas Lake region of Michigan. Mich. Bot. **5:** 99–108. 1966c. [*R. palustris* var. *Fernaldiana* and var. *hispida.*]

———. Taxonomy and distribution of the genus *Rorippa* (Cruciferae) in North America. Sida **4:** 279–430. 1972. [Treatment of 22 indigenous and seven introduced species; descriptions, distributions (no specimens cited), evolutionary relationships of some species, keys, 22 maps, index; *Nasturtium* as a distinct genus.]

TAYLOR, R. L., & B. MACBRYDE. New taxa and nomenclatural changes with respect to vascular plants of British Columbia: a descriptive resource inventory. Canad. Jour. Bot. **56:** 184–195. 1978. [*R. palustris* subsp. *Fernaldiana* var. *glabra,* 185, 186.]

THIERET, J. W. Twenty-five species of vascular plants new to Louisiana. Proc. Louisiana Acad. Sci. **32:** 78–82. 1969. [*R. Nasturtium-aquaticum,* 79.]

THOMMEN, G. H., & D. F. WESTLAKE. Factors affecting the distribution of populations of *Apium nodiflorum* and *Nasturtium officinale* in small chalk streams. Aquatic Bot. **11:** 21–36. 1981. [Life cycle, overwintering, growth rates, regeneration, competition.]

TOMŠOVIC, P. Die wichtigsten Ergebnisse der Revision tschechoslowakischer Sumpfkressen (*Rorippa* Scop. em. Reichenb.). (In Czech; English and German summaries.) Preslia **41:** 21–38. *figs. 3, 5, 7, 8, 10.* 1969. [*R. amphibia, R. austriaca, R. palustris* (as *islandica*), *R. pyrenaica, R. sylvestris*; variation, morphology, interspecific hybrids, distributions.]

———. Zur Vorkommen seltener *Rorippa*-Arten in Österreich (mit Bemerkungen zu ihren Arealgrenzen). *Ibid.* **43:** 338–343. 1971.

———. The diploid *Rorippa islandica* discovered in southern Europe. Folia Geobot. Phytotax. **9:** 209–212. 1974.

TURRILL, W. B. *Rorippa pyrenaica* and closely related species. Bull. Soc. Bot. Bulgaria **4:** 48–56. 1931.

VALENTINE, D. H. *Rorippa, Nasturtium. In:* T. G. TUTIN *et al.,* eds., Fl. Europaea **1:** 283–285. 1964.

VASSILCHENKO, I. T. *Rorippa. In:* V. L. KOMAROV & N. A. BUSCH, eds., Fl. USSR **8:** 135–141. 1939. [English translation by R. LAVOOTT, **8:** 103–107. Jerusalem. 1970.]

VILLANI, A. Dei nettarii di alcune specie di *Nasturtium* (L.) R. Br. Nuovo Giorn. Bot. Ital. II. **19:** 499–506. *pl. 16.* 1912.

VINCENT, W. F., & M. T. DOWNES. Variation in nutrient removal from a stream by watercress (*Nasturtium officinale* R. Br.). Aquatic Bot. **9:** 221–235. 1980.

WILSON, C. L. Adventitious roots and shoots in an introduced weed. Bull. Torrey Bot. Club **54:** 35–38. 1927. [*R. austriaca*; exogenous origin of shoots and adventitious roots.]

WUNDERLIN, R. P. Guide to the vascular plants of central Florida. 472 pp. Tampa and other cities, Florida. 1982. [*Nasturtium,* 194; *Rorippa,* 195.]

YARNELL, S. H. Cytogenetics of the vegetable crops. II. Cruciferae. Bot. Rev. **22:** 81–166. 1956. [*R. Nasturtium-aquaticum* (as *N. officinale*), 153.]

36. **Armoracia** Gaertner, Meyer, & Scherbius, Oek.-Techn. Fl. Wetterau **2:** 426. 1800, nom. cons.

Glabrous, perennial herbs of aquatic, semiaquatic, or somewhat mesic habitats. Roots much branched, usually coarse, woody or somewhat fleshy, sometimes slender and adventitious from rootstocks. Stems usually unbranched at base, up to 2 m high. Basal leaves short or long petiolate, small or to 1 m long, crenate or dentate to serrate; middle cauline leaves short petiolate to subsessile, crenate to laciniate or pinnatisect, or (when submersed) 1–4 times pinnately or dichotomously dissected into numerous capillary to narrowly linear segments; uppermost or emersed cauline leaves serrate to serrulate or crenate to entire. Inflorescence an ebracteate raceme or panicle, greatly elongated in fruit;

fruiting pedicels ascending or divaricate to slightly reflexed. Sepals oblong to ovate, spreading, glabrous, nonsaccate at base, membranaceous at margin. Petals white, oblong or oblanceolate to spatulate [or broadly obovate], short clawed. Nectar glands flat, united into a ring surrounding bases of the lateral stamens and subtending those of the median ones. Stamens 6, slightly tetradynamous; filaments somewhat spreading, slightly dilated at base, not appendaged; anthers linear or oblong to ovate, sagittate at base. Fruits glabrous, oblong to obovoid or subglobose, sessile or short stipitate, flattened parallel or perpendicular to the septum; valves nerveless; septum usually with a central perforation, sometimes reduced to a narrow rim along the interior of replum; styles conspicuous and nearly as long as the fruit or short [to obsolete]; stigmas capitate, entire or slightly 2-lobed, usually much wider than the style. Seeds numerous, turgid, wingless, reticulate, biseriately arranged, nonmucilaginous when wet; cotyledons accumbent. Base chromosome number 8. (Including *Raphanis* Moench, nom. rejic.; *Neobeckia* Greene.) TYPE SPECIES: *A. rusticana* Gaertner, Meyer, & Scherb. (*Cochlearia Armoracia* L.). (Generic name is an ancient Greek name for horseradish. However, Courter & Rhodes suggested that the name is derived from Celtic *ar,* near, *mor,* the sea, and *rich,* against, meaning a plant growing near the sea. The word horseradish suggests a coarse or very strong radish, as distinguished from the edible radish, *Raphanus sativus* L. (Rosengarten).)—HORSERADISH.

A genus of four species distributed in eastern and southeastern Europe and Siberia, and disjunctly in the eastern and central United States. *Armoracia* is represented in the southeastern United States by two species, one of which is indigenous.

Armoracia rusticana Gaertner, Meyer, & Scherb.[13] (*Cochlearia Armoracia* L., *Nasturtium Armoracia* (L.) Fries, *Radicula Armoracia* (L.) Robinson, *Rorippa Armoracia* (L.) Hitchc., *Armoracia Armoracia* (L.) Britton, *A. lapathifolia* Gilib., *A. sativa* Bernh., *Cochlearia rusticana* Lam., *Rorippa rusticana* (Lam.) Gren. & Godron), horseradish, $2n = 32$, is a native of temperate eastern Europe from the Caspian Sea north into Russia, Poland, and southern Finland. It is an escape from cultivation and a widely naturalized weed throughout most of Europe and central and northern North America. It usually grows in moist habitats along ditches, riverbanks, and roadsides, as well as in waste grounds, fields, and disturbed sites. Uncommon in the Southeastern States, it has been reported from North Carolina and Tennessee.

Armoracia rusticana is very closely related to *A. macrocarpa* (Waldst. & Kit.) Kit. ex Baumg., a marsh plant of the central Danube Basin (Hungary, Yugoslavia, and probably Rumania), and to *A. sisymbrioides* (DC.) Cajander, a wet-meadow or sometimes aquatic plant of Siberia and Sachalin. From these, *A. rusticana* differs mainly in its smaller flowers and fruits. However, it rarely produces fruits with fully developed seeds. It may have evolved through domestication from ancestors not too different from *A. macrocarpa* and *A. sisymbrioides,* both of which are used occasionally as a substitute for horseradish.

[13] For detailed nomenclature of the species, see Fosberg (1965, 1966), Lawrence (1953, 1971), and McVaugh.

Armoracia rusticana rarely sets seeds in cultivation because it is a self-incompatible crop plant that is propagated by root cuttings originally derived from a few plants. Its high sterility is also caused by several meiotic irregularities, reduced pollen fertility (sometimes as low as 20 percent), abortion of ovules, failure of fertilization, endosperm–maternal tissue incompatibility, or embryo mortality (Stokes). On the basis of these anomalies, several authors (e.g., Lawrence, 1971) have suggested that *A. rusticana* is a hybrid, the ancestral parents of which are unknown. Meiotic irregularities, such as the lagging and partial pairing of chromosomes, may support the hybrid origin of horseradish (Weber), but the evidence is tenuous and more research is needed to confirm such an origin. Dore suspected that *A. rusticana* is a polyploid variant of *A. macrocarpa,* but both are tetraploids based on $x = 8$. Easterly's report of $n = 14$ for the former species is apparently in error.

The North American *Armoracia lacustris* (A. Gray) Al-Shehbaz & V. Bates (*Nasturtium lacustre* A. Gray, *Cochlearia Armoracia* L. var. *aquatica* Eaton, *C. aquatica* (Eaton) Eaton, *N. natans* DC. var. *americanum* A. Gray, *A. americana* (A. Gray) W. J. Hooker, *Rorippa americana* (A. Gray) Britton, *Neobeckia aquatica* (Eaton) Greene, *Radicula aquatica* (Eaton) Robinson, *A. aquatica* (Eaton) Wieg., *Rorippa aquatica* (Eaton) Palmer & Steyerm.), lake cress, river cress, grows in quiet waters in streams, springs, rivers, ponds, and lakes, as well as on muddy shores, mud flats, and floodplains (W. M. Countryman, pers. comm.). It is distributed exclusively east of the 95th meridian from Quebec south into Florida, west into eastern Texas, and north into eastern Oklahoma, Missouri, Iowa, Minnesota, Wisconsin, Michigan, and southern Ontario. *Armoracia lacustris* is sporadic in the Southeast but has been recorded from all of the Southeastern States except the Carolinas (see Al-Shehbaz & Bates for distribution data by county). Beal indicated that the species was reported from North Carolina, but neither he nor I have seen any specimens from this state.

The submersed leaves of *Armoracia lacustris* are pinnately or dichotomously dissected into numerous filiform segments, while the emersed ones have dentate margins. Submersed leaves near the water surface show a gradual transition between these two leaf types. Heterophylly in *A. lacustris,* unlike that in *Proserpinaca palustris* L. (Haloragaceae), is not controlled by photoperiodism and appears to be related to the fluctuation of temperature (C. E. Wood, Jr., pers. comm.). Gray was the first to observe that the submersed leaves of *A. lacustris* fall off readily as the plant is removed from water. Dissected leaves are usually detached in nature during late summer and fall. They float and are transported by water currents; within a week they produce at the petiolar end adventitious roots, a cluster of tiny, undivided leaves, and a small shoot. The new plantlet eventually sinks to the bottom, and the remainder of the leaf degenerates.

Armoracia lacustris is remarkable for its capacity to regenerate plants from tiny fragments of leaves, stems, and roots. According to La Rue, the species (as *Radicula aquatica*) reproduces only vegetatively and has not been found to produce seeds at upper latitudes. In warmer areas, however, the plant occasionally reproduces sexually. It is possible that *A. lacustris* is self-incompatible and that most of the local "populations" are merely clones. Young plants, plantlets, and stem bases of older plants remain alive during the winter and produce new rosette leaves and shoots in the spring.

Although *Armoracia rusticana* is capable of forming new plants from small root fragments, its capacity for regeneration is apparently confined to the area of lateral-root traces (Lindner). The species produces pinnatifid leaves apparently only during the early and late parts of the growing season (Davis).

Earlier authors (e.g., De Candolle, 1821; Bentham & Hooker) reduced *Armoracia* to a section of *Cochlearia* L., but it is now believed that these genera are unrelated and that the latter belongs to the tribe Lepidieae. With the exception of Schulz, who placed *Armoracia* in the tribe Drabeae, most recent authors follow Von Hayek in associating the genus closely with *Rorippa. Armoracia* differs from *Rorippa* in having an incomplete or rudimentary septum (see FIGURE 1m) and flattened fruits. It is distinguished by its white flowers from all rorippas that it resembles by having fruits less than three times longer than broad. It is evident that the boundaries between these closely related genera are not sharply defined, but such a situation is often encountered throughout the Cruciferae.

Whether *Armoracia lacustris* and the *A. rusticana* complex are congeneric or should be placed in different genera is debatable. Rickett (p. 236) believed that they "seem to have nothing in common except that they are both crucifers," and Schulz placed them in different tribes, the former as *Nasturtium* (Arabideae) and the latter as *Armoracia* (Drabeae). The two species share several technical characters that support their placement in one genus (Al-Shehbaz & Bates).

Armoracia rusticana has been extensively surveyed for flavonoids and particularly for root glucosinolates. The hydrolysis products of the latter compounds are the flavoring principles in the commercial horseradish. The pungent taste is attributed to allyl isothiocyanate, which constitutes more than 60 percent of these products. Other important compounds are 2-butyl, 3-butenyl, 4-pentenyl, and 2-phenyl glucosinolates. A total of 30 root glucosinolates (including six new ones and excluding two doubtful compounds reported by Gilbert & Nursten) have been identified by Grob & Matile. This high number of glucosinolates exceeds the number previously isolated in any one species.

The fleshy outer part of the mature root of *Armoracia rusticana* is derived either directly or indirectly from the pericycle. The cork cambium produces a few layers of cork and a broad, spongy phylloderm with axially elongated parenchymatous cells that are mixed with isolated stone cells near the cambium. Roots are capable of regeneration only after the cortex is shed and the periderm is fully developed. Bud primordia are initiated from meristems derived from the cork cambium in areas of the lateral root scars.

Armoracia rusticana has been cultivated for some 2000 years (Rosengarten). The grated root, mixed with vinegar, salt, and oil, is a pungent condiment that is used with roast beef, fish, lamb, and ham. It is one of five "bitter herbs" eaten by Hebrews during Passover (Courter & Rhodes). Several medicinal properties have been attributed to horseradish. It has been used as a stimulant, antiscorbutic, diuretic, aphrodisiac, rubefacient, expectorant, and diaphoretic, as well as a remedy for dropsy, rheumatism, and neuralgia. Horseradish can be a noxious weed that is extremely difficult to eradicate because small root fragments are capable of regenerating new plants. Kingsbury indicated that poisoning of horses, cattle, and swine has resulted from feeding on the plant. *Armoracia sisymbrioides* is cultivated in Siberia for its roots, which are used as a substitute for horseradish (Busch).

REFERENCES:

Under family references in AL-SHEHBAZ (Jour. Arnold Arb. **65**: 343–373. 1984), see BENTHAM & HOOKER; BRITTON & BROWN; DE CANDOLLE (1821, 1824); CRISP; EASTERLY (1963); FERNALD; VON HAYEK; JANCHEN; KINGSBURY; KNUTH; MANTON; MARKGRAF; MURLEY; PATMAN & ILTIS; RICKETT; ROLLINS (1981); SCHULZ; SMALL; E. B. SMITH; and YARNELL.

Under tribal references see AL-SHEHBAZ (1977); BEAL; BOLKHOVSKIKH *et al.*; CHESTER; CLEWELL; CORBETT; CORRELL & CORRELL; DUNCAN & KARTESZ; ELLIS *et al.*; FASSETT; FREEMAN *et al.*; GATTINGER; GODFREY & WOOTEN; GOLDBLATT (1984); HEBEL; JONES (1975); KJAER; MACROBERTS; NIELSEN *et al.*; PATMAN; PULLEN *et al.*; and SMALL.

AL-SHEHBAZ, I. A., & V. BATES. *Armoracia lacustris* (Brassicaceae), the correct name for the North American lake cress. Jour. Arnold Arb. **68**: 357–359. 1987.

BALL, P. W. *Armoracia. In:* T. G. TUTIN *et al.*, eds., Fl. Europaea **1**: 284. 1964. [*A. macrocarpa, A. rusticana.*]

BUSCH, N. A. *Armoracia. In:* V. L. KOMAROV & N. A. BUSCH, eds., Fl. USSR **8**: 141–143. 1939. [English translation by R. LAVOOTT, **8**: 107–109. Jerusalem. 1970.]

CANDOLLE, A. DE. Sur le nom et l'origine du cran (*Cochlearia rusticana,* Lamk.), appelé improprement *Armoracia* ou cran de Bretagne. Revue Hort. **1852**: 172–176. 1852.

CHISHOLM, M. D., & M. MATSUO. Biosynthesis of allylglucosinolate and 3-methylthiopropylglucosinolate in horseradish, *Armoracia lapathifolia.* Phytochemistry **11**: 203–207. 1972.

COURTER, J. W., & A. M. RHODES. Historical notes on horseradish. Econ. Bot. **23**: 156–164. 1969. [Origin, earlier and recent vernacular names, uses, sterility, culture.]

DAVIDSON, R. A. The vascular flora of southeastern Iowa. State Univ. Iowa Stud. Nat. Hist. **20**(2): 1–102. 1959. [*A. lacustris* (as *aquatica*), *A. rusticana,* 53.]

DAVIS, C. A. The pinnatifid leaves of *Nasturtium Armoracia.* Bull. Torrey Bot. Club **17**: 318, 319. 1890.

DORE, J. Studies in the regeneration of horseradish. I. A re-examination of the morphology and anatomy of regeneration. Ann. Bot. II. **19**: 127–137. 1955.

——— & W. T. WILLIAMS. Studies in the regeneration of horseradish. II. Correlation phenomena. Ann. Bot. II. **20**: 231–249. *pl. 7.* 1956. [Initiation of buds and roots, differentiation, role of auxins.]

ELSTNER, E. F., & A. HEUPEL. Formation of hydrogen peroxide by isolated cell walls from horseradish (*Armoracia lapathifolia* Gilib.). Planta **130**: 175–180. 1976.

FOERSTE, A. F. Botanical notes. Bull. Torrey Bot. Club **16**: 266–268. *pl. 94.* 1889. [*A. lacustris* (as *Nasturtium*); formation of plantlets from detached submersed leaves.]

FOSBERG, F. R. Nomenclature of the horseradish (Cruciferae). Baileya **13**: 1–4. 1965. [Taxonomic history, nomenclature.]

———. The correct name of the horseradish (Cruciferae). *Ibid.* **14**: 60. 1966. [Correct name is *A. rusticana* (1800), not *A. lapathifolia* (1793), because the latter was a renaming of *Cochlearia Armoracia* in an invalidly published generic name.]

FURSA, N. S. Flavonoids of *Armoracia rusticana* Gaertn., Mey. et Scherb. and *A. sisymbrioides* (DC.) Cajand. (In Russian.) Rastit. Resur. **19**: 74–78. 1983.*

———, V. I. LITVINENKO, & P. E. KRIVENCHUK. Flavonoids of *Armoracia rusticana* and *Barbarea arcuata.* (In Russian.) Khim. Prir. Soedin. **1969**: 320. 1969. [*A. rusticana* contains kaempferol and quercetin.]

GILBERT, J., & H. E. NURSTEN. Volatile constituents of horseradish roots. Jour. Sci. Food Agr. **23**: 527–539. 1972.

GORECKA, K., W. SRZEDNICKA, & L. S. JANKIEWICZ. Tissue culture of horseradish meristems: sterilization of buds and comparison of media. Acta Agrobot. **31**: 195–204. 1979.*

GRAY, A. A notice of some new, rare, or otherwise interesting plants, from the northern and western portions of the state of New York. Ann. Lyc. Nat. Hist. N. Y. **3**: 221–238. 1835. [*A. lacustris* (as *Nasturtium natans β americanum*), 223.]

GREENE, E. L. New or noteworthy species.—XVII. Pittonia **3**: 91–116. 1896. [*Neobeckia aquatica,* 95, 96.]

GROB, K., JR., & P. MATILE. Capillary GC of glucosinolate-derived horseradish constituents. Phytochemistry **19**: 1789–1793. 1980.

ISAAC, O., & E. KOHLSTAEDT. Beitrag zur Kenntnis des ätherischen Meerrettichöls. Arch. Pharm. **295**: 165–173. 1962. [Mustard oils of *A. rusticana* (as *Cochlearia Armoracia*).]

JØRGENSEN, L. B., H.-D. BEHNKE, & T. J. MABRY. Protein-accumulating cells and dilated cisternae of the endoplasmic reticulum in three glucosinolate-containing genera: *Armoracia, Capparis, Drypetes.* Planta **137**: 215–224. 1977. [Ultrastructure of myrosin idioblasts.]

KIRSO, U., & D. STOM. Cooxidation of carcinogenic benzo (α) pyrene and phenols by horseradish pyroxidase (*Armoracia lapathifolia*). Detoxification of environment. Acta Hydrochem. Hydrobiol. **9**: 427–432. 1981.*

LA RUE, C. D. Regeneration in *Radicula aquatica.* Pap. Michigan Acad. Sci. Arts Lett. I. **28**: 51–61. 1943. [*A. lacustris*; habit, habitat, vegetative reproduction, regeneration of various plant parts, hormones.]

LAWRENCE, G. H. M. Correct name of the horse-radish. Baileya **1**: 11. 1953. [See FOSBERG (1965, 1966).]

———. The horseradish *Armoracia rusticana.* Herbarist **37**: 17–19. 1971. [Vernacular and scientific names, use.]

LINDNER, R. C. Factors affecting regeneration of the horseradish root. Pl. Physiol. **15**: 161–181. 1940. [Effects of temperature and auxins, initiation of buds on isolated pieces of root.]

MAC DOUGAL, D. T. The determinative action of environic factors upon *Neobeckia aquatica* Greene. Flora **106**: 264–280. 1914. [Influence of environment, variation, vegetative reproduction, regeneration.]

MCVAUGH, R. Questionable validity of names published in Gilibert's floras of Lithuania. Gent. Herb. **8**: 83–90. 1949. [*A. lapathifolia,* 90.]

MOYLE, J. B., & N. HOTCHKISS. The aquatic and marsh vegetation of Minnesota and its value to waterfowl. Minnesota Dep. Conserv. Tech. Bull. **3**. 122 pp. 1945. [*A. aquatica,* 55.]

NJOKU, E. Leaf heteromorphism in *Cochlearia Armoracia.* Unpubl. M.Sc. thesis, Univ. Manchester, U. K. 1948.*

OGDEN, E. C. Anatomical patterns of some aquatic vascular plants of New York. New York State Mus. Bull. **424**. v + 133 pp. 1974. [*A. aquatica,* 22, *map 154, pl. 48.*]

OLDHAM, C. H. *Brassica* crops and allied cruciferous crops. 295 pp. London. 1948. [*A. rusticana*; cultivation, planting, marketing, 168–172.]

RAUSCHERT, S. Vorschlag zur Konservierung des Gattungsnamens 2965. *Armoracia* Gaertner, Meyer, Scherbius (1800) vs. *Raphanis* Moench (1794) und *Armoracia* Bernhardi (1800) [Cruciferae]. Taxon **17**: 231, 232. 1968.

RHODES, A. M. Horseradish—problems and research in Illinois. Pp. 137–148 *in* D. S. SEIGLER, ed., Crop resources. New York, San Francisco, and London. 1977. [Culture, breeding, diseases, processing, storage, insect infestations.]

———, J. W. COURTER, & M. C. SHURTLEFF. Identification of horseradish types. Trans. Illinois Acad. Sci. **58**: 115–122. 1965. [Thirty cultivars grouped in three types on the basis of leaf morphology and resistance to white rust and turnip-mosaic virus.]

ROSENGARTEN, F., JR. The book of spices. *Frontisp.* + xiii + 489 pp. Wynnewood, Pennsylvania. 1969. [*A. rusticana,* 268–273.]

SCHEEL, H. Untersuchungen an Primär und Sekundärwurzeln von *Armoracia lapathifolia* Gilib. unter besonderer Berücksichtigung des sekundären Dickenwachstums. Wiss. Zeitschr. Päd. Hochsch. Potsdam **19:** 45–58. 1975.* [Related papers in *ibid.* **16:** 27–44. 1972* and **18:** 21–31. 1974.*]

SCOGGAN, H. J. *Armoracia.* Fl. Canada **3:** 798, 799. 1978.

SMITH, P. M. Minor crops. Pp. 301–324 *in* N. W. SIMMONDS, ed., Evolution of crop plants. London and New York. 1976. [*A. rusticana,* 305, 306.]

STOKES, G. W. Seed development and failure in horseradish. Jour. Hered. **46:** 15–21. 1955.

WEBER, W. W. Seed production in horseradish. Jour. Hered. **40:** 223–227. 1949.

WIEGAND, K. M. Some changes in nomenclature. Rhodora **27:** 186, 187. 1925. [*A. aquatica.*]

WILLIAMS, W. T., J. DORE, & D. G. PATTERSON. Studies in the regeneration of horseradish. III. External factors. Ann. Bot. II. **21:** 627–632. 1957. [Effects of temperature, moisture, oxygen, and carbon dioxide.]

ZÁBORSKÝ, J. *In:* J. MÁJOVSKÝ *et al.,* eds., Index of chromosome numbers of Slovakian flora (part 3). Acta Fac. Nat. Comen. Bot. **22:** 1–20. 1974. [*A. macrocarpa,* 3; $2n = 32$.]